SOINS MATERNELS CHEZ L'OURS BRUN SCANDINAVE DANS UN CONTEXTE DE CHASSE INTENSIVE

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Thèse présentée au Département de biologie en vue
de l'obtention du grade de docteur ès sciences (Ph.D.)

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UNIVERSITÉ DE SHERBROOKE

Sherbrooke, Québec, Canada, juillet 2020

Le 15 juillet 2020

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À ma mère

et son amour des mots et des connaissances

REMERCIEMENTS

D’un bon jour, j’ai osé envoyer un courriel que je croyais futile, mais qui s’avéra le début d’une aventure d’une ampleur que je n’avais pas imaginée. Du haut de mes petites expériences, mais de mes grandes espérances, j’ai demandé à discuter d’un projet de doctorat potentiel avec Fanie Pelletier. Elle m’a donné une chance de (me) prouver qu’une carrière en recherche était ma voie. J’ai reçu un encadrement exemplaire alliant liberté et un juste niveau d’appui, me permettant de transformer certaines de mes insécurités en confiance. Merci beaucoup, Fanie. Je remercie aussi mon co-directeur, Andreas Zedrosser, d’avoir toujours considéré avec grand respect et intérêt toutes mes inquiétudes, questions et idées. Andreas, thank you for trusting Fanie and taking this leap of faith with me.

J’ai eu l’honneur de partager cette aventure avec plusieurs collaborateurs inspirants: Jon Swenson, Gabriel Pigeon, Martin Leclerc, Sam Steyaert et Richard Bischof. D’autres m’ont aussi aidée dans mes réflexions : Dany Garant, Marco Festa-Bianchet, Anne Hertel et Shane Frank. Merci aussi aux membres des laboratoires Pelletier, Garant et Festa-Bianchet pour nos échanges et votre amitié, et plus particulièrement à mes amies Philippine Gossieaux et Pauline Toni. Merci à tous ceux qui ont contribué à la collecte de données et surtout à Sven Brunberg et sa connaissance légendaire des ours et Andrea Friebe pour l’accès aux données. Les organismes suivants ont contribué à la réalisation de ce projet : CRSNG et FRQ-NT, CSBQ, CEN, CRC, MEES et EnviroNord.

Finalement, merci à mon fils de me rappeler à la réalité et m’enseigner la reconnaissance, l’indulgence, le lâcher prise et l’essentiel du bonheur. Je m’y exerce. Merci à ma mère, qui n’a malheureusement pas pu suivre mon cheminement, mais dont la mémoire continue de guider mes actions. Elle aurait aimé me voir aller loin. Je crois que j’y suis. Et surtout, merci à mon amoureux, Rémi, qui est un pilier sur lequel repose mes réalisations. Merci pour ton amour, ta patience, ta compréhension et ton ouverture merveilleuse sur un monde inconnu.

SOMMAIRE

Afin d'assurer la pérennité de leurs gènes dans la population, les individus doivent maximiser leur survie et leur reproduction. Les ressources étant toutefois limitées, les individus doivent faire des compromis dans leurs décisions d'allocation d'énergie entre ces fonctions. Ainsi, un investissement dans la reproduction courante se fait au détriment d'un investissement futur dans la reproduction ou la survie. Les individus doivent adopter des tactiques de reproduction leur procurant un ratio bénéfices/coûts optimal dans un contexte évolutif et environnemental donné. À ce titre, les soins parentaux (principalement *maternels*) permettent d'améliorer la valeur adaptative des jeunes, mais ils sont coûteux pour les parents. Leur durée présente toutefois une grande variabilité inter et intraspécifique, ce qui suggère qu'elle peut être ajustée en fonction de facteurs intrinsèques (p. ex. condition corporelle des jeunes), ou extrinsèques (p. ex. conditions environnementales). Comme la durée des soins maternels peut influencer les taux de reproduction individuels et populationnels, il importe alors d'identifier les causes et les conséquences démographiques de la variation dans ce trait afin d'anticiper la réponse des populations animales sauvages face à un changement potentiel dans ce trait d'histoire de vie.

L'objectif général de cette thèse était d'étudier les compromis d'allocation des ressources à la reproduction, d'identifier les déterminants de la durée des soins maternels et de mesurer les conséquences individuelles et populationnelles de la variation dans ce trait chez l'ours brun (*Ursus arctos*) Scandinave. Cet objectif a été réalisé en se basant sur les données de reproduction et de survie issues du suivi à long-terme (>30 ans) de l'ours brun en Scandinavie récoltées par le Scandinavian Brown Bear Research Project. La durée des soins maternels dans cette population est de soit 1,5 ans (soins courts) ou 2,5 ans (soins longs). De plus, cette population vit dans un paysage dominé par l'activité humaine et offre ainsi une belle opportunité de s'intéresser aux variations dans les tactiques de reproduction maternelles dans un contexte environnemental particulier pouvant influencer la balance entre coûts et bénéfices.

En allouant de l'énergie à la reproduction actuelle, les parents ont moins d'énergie pour leurs reproductions futures. Ce compromis se manifeste aussi au sein d'un seul évènement de reproduction chez les espèces produisant plus d'un jeune à la fois. En effet, les ressources étant limitées, les parents ne peuvent produire un nombre maximal de jeunes de taille maximale; ils doivent soit produire un petit nombre de grands jeunes ou un grand nombre de jeunes de plus petite taille. Toutefois, compte tenu de la grande variation en masse observée intra-portée en nature, ce compromis entre taille et nombre de jeunes n'est potentiellement pas homogène; certains jeunes pourraient en payer le prix. Dans le chapitre 2, j'ai montré que la diminution de la masse des jeunes avec l'augmentation de la taille de portée est inégale chez l'ours brun. En effet, dans les grandes portées, seuls les plus petits oursons ont une masse réduite. Ce résultat suggère que les femelles ours brun utilisent une stratégie conservatrice de reproduction en maintenant un investissement stable dans une fraction de leur portée.

Des études théoriques et empiriques montrent que la masse des jeunes (ainsi que ses déterminants) est un élément central sur lequel les femelles pourraient baser leur 'décision' de poursuivre ou non les soins maternels, mais les relations de causalité sont peu connues. Au chapitre 3, j'ai étudié les causes de variation dans la durée des soins maternels chez l'ours brun et j'ai montré que ces dernières diffèrent entre les populations au nord et au sud de la Suède. La masse des oursons n'est importante qu'au nord, là où les conditions environnementales sont moins favorables. Au sud, la plus forte densité d'ours et la plus grande pression anthropique pourraient expliquer l'absence de relation attendue. Effectivement, j'ai montré au chapitre 4 qu'il est important de considérer les conflits sexuels et le potentiel des mâles de provoquer la séparation des groupes familiaux (femelles et jeunes dépendants). Les femelles ayant un plus faible risque de rencontrer des mâles adultes (patrons de sélection d'habitats différents) durant la période d'accouplements procuraient des soins maternels longs. Ces femelles utiliseraient aussi la proximité aux habitations humaines comme bouclier et tactique d'évitement des mâles. Les femelles pourraient donc tirer avantage d'un paysage dominé par l'Homme pour moduler leurs tactiques de reproduction. Au chapitre 5, j'ai montré que la sélection induite par la chasse pourrait influencer l'occurrence relative des tactiques de

reproduction dans la population du sud de la Suède. En effet, j'ai montré que la forte pression de chasse à l'ours et sa réglementation interdisant de tuer des membres de groupes familiaux procure un bénéfice en survie aux femelles procurant des soins maternels longs. J'ai aussi montré que la durée des soins maternels est un trait répétable et que la sélection induite par la chasse pourrait expliquer l'augmentation de la proportion de portées ayant reçu des soins maternels longs au cours des 20 dernières années dans la population. Pour les femelles procurant des soins maternels longs, les bénéfices en survie compenseraient pour les coûts en reproduction à forte pression de chasse. J'ai montré, à l'aide de modèles de dynamique de population, que grâce à cette compensation, un changement en tactique de reproduction n'affecterait pas le taux de croissance de la population à pression de chasse moyenne. Un tel changement affecterait plutôt la structure d'âge et le temps de génération de la population.

Cette thèse apporte une importante contribution à notre compréhension jusqu'alors limitée des déterminants intrinsèques et extrinsèques de la durée des soins maternels. Elle montre l'importance de considérer l'hétérogénéité phénotypique dans les compromis d'allocation de ressources à la reproduction et les tactiques de reproduction. Elle montre aussi l'importance de tenir compte du contexte environnemental dans lequel vivent les individus pour évaluer les coûts et bénéfices associés aux différentes tactiques de reproduction. Surtout, elle montre que l'activité humaine a le potentiel de modifier les comportements maternels, et ce, de façon surprenante. Dans un contexte où les activités humaines s'intensifient aux échelles locale et planétaire, cette thèse montre qu'il est important de considérer l'Homme et les effets de ses activités dans l'évaluation de la dynamique des populations animales sauvages.

Mots clés : Soins maternels, compromis d'histoire de vie, conflits sexuels, sélection induite par l'Homme, chasse, dynamique de population

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GPS	Système de positionnement global (*Global Positioning System*)
GSM	Système global pour communication mobile (*Global System for Mobile communication*)
ISS(SSI)	Infanticide Sexuellement Sélectionné (*Sexually Selected Infanticide*)
SBBRP	Projet de Recherche sur l'ours brun scandinave (*Scandinavian Brown Bear Research Project*)
VHF	Très haute fréquence (*Very High Frequency*)

CHAPITRE 1
INTRODUCTION

1.1 La théorie sur les histoires de vie et les compromis

Les traits d'histoire de vie caractérisent l'histoire de vie des individus et sont en lien avec deux grandes composantes de la valeur adaptative : la survie et la reproduction (Stearns, 1992). L'âge à la première reproduction, le nombre et la taille des jeunes produits, la survie âge-spécifique et la longévité sont des exemples de traits d'histoire de vie. Afin d'améliorer la représentation de leurs gènes dans les générations futures (c.-à-d. leur valeur adaptative; Westneat et Fox, 2010), les individus doivent maximiser leurs chances de survie et leur taux de reproduction en optimisant la valeur de ces traits d'histoire de vie.

Toutefois, les traits d'histoire de vie ne s'expriment pas de façon indépendante puisqu'ils sont liés par des relations négatives, d'ordres génétiques ou phénotypiques, appelées « compromis d'histoire de vie » (Stearns, 1992). Un compromis se traduit par un coût en valeur adaptative lorsqu'une augmentation bénéfique de la valeur d'un trait se produit au détriment d'un autre trait (Stearns, 1989). Puisque les ressources dont disposent les animaux sauvages sont limitées, des compromis surviennent lorsque les décisions d'allocation des ressources entre deux ou plusieurs fonctions entrent en compétition. Un exemple de compromis est celui entre la taille et le nombre de jeunes produits (sujet abordé au chapitre 2) puisqu'avec une quantité donnée d'énergie, les parents ne peuvent que produire soit un grand nombre de jeunes de petite taille ou un petit nombre de jeunes de grande taille (Charnov et Ernest, 2006). Les compromis dans les traits d'histoire de vie sont largement étudiés en écologie évolutive et les principaux concernent : l'âge et la taille à la maturité sexuelle et les coûts de la reproduction; c'est-à-dire les relations négatives entre la

reproduction actuelle et la survie ou la reproduction future (Williams, 1966; Trivers, 1972; Pianka, 1976). Les stratégies de reproduction sont le programme génétique à la base des décisions d'allocation des ressources aux différentes fonctions et le phénotype qui en résulte s'appelle une « tactique de reproduction » (Gross, 1996).

Les compromis dans les traits d'histoire de vie et les coûts de la reproduction ne sont toutefois pas toujours observés en nature (Stearns, 1989). Par exemple, des résultats contradictoires sont rapportés dans la littérature concernant le compromis entre le nombre et la taille des jeunes (Bernardo, 1996). Les compromis dans les traits d'histoire de vie peuvent être masqués par des différences individuelles dans l'acquisition et l'allocation des ressources et par l'absence de contraintes dans la disponibilité des ressources (van Noordwijk et de Jong, 1986; Hamel *et al.*, 2010). Il importe donc de considérer cette hétérogénéité individuelle dans l'évaluation des compromis dans les traits d'histoire de vie et des tactiques de reproduction (Hamel *et al.*, 2009; Festa-Bianchet *et al.*, 2019).

La combinaison des traits d'histoire de vie est caractéristique d'une espèce et est le résultat de son histoire évolutive et des pressions de sélection environnementales auxquelles l'espèce doit faire face. Généralement, dans un environnement où la pression de mortalité est indépendante du génotype des individus (c.-à-d. mortalité extrinsèque), la sélection naturelle devrait favoriser une plus grande fécondité (Pianka, 1976). On parle alors de sélection, ou d'une stratégie de reproduction, de type « *r* » où *r* réfère au taux intrinsèque maximal de croissance naturelle, r_{max}. À l'inverse, lorsque la pression de mortalité extrinsèque est faible, une plus grande allocation d'énergie à la maintenance et à la production de peu de jeunes très performants devrait être favorisée, ce que l'on appelle la sélection, ou une stratégie de reproduction, de type « *K* », où *K* réfère à la capacité de support du milieu (Pianka, 1970). On peut ainsi imaginer un continuum, allant de *r* à *K*, le long duquel les espèces occupent une position donnée (Figure 1.1). Par exemple, la stratégie de reproduction des grands mammifères est majoritairement de type *K* puisque ces

derniers ont de faibles taux de reproduction, bénéficient d'une très grande probabilité de survie (Gaillard *et al.*, 2000) et leur succès reproducteur à vie est surtout influencé par leur longévité (p. ex. chez l'ours brun; Zedrosser *et al.*, 2013). Puisque la valeur adaptative est davantage influencée par la survie plutôt que la reproduction chez les grands mammifères, l'énergie devrait être davantage allouée à la maintenance qu'à la reproduction (Stearns, 1992), selon une stratégie conservatrice (Festa-Bianchet *et al.*, 2019). La vitesse d'histoire de vie d'une espèce se substitue souvent aux termes *r* et *K* (p. ex. Hamel *et al.*, 2010). Selon cette terminologie, les grands mammifères se positionneraient à l'extrémité droite du gradient entre histoires de vie lentes et rapides (Figure 1.1). De façon plus générale, on peut également parler de syndromes de train de vie caractéristiques des vitesses d'histoire de vie lentes et rapides, ce qui inclus des traits comportementaux et physiologiques (Réale *et al.*, 2010).

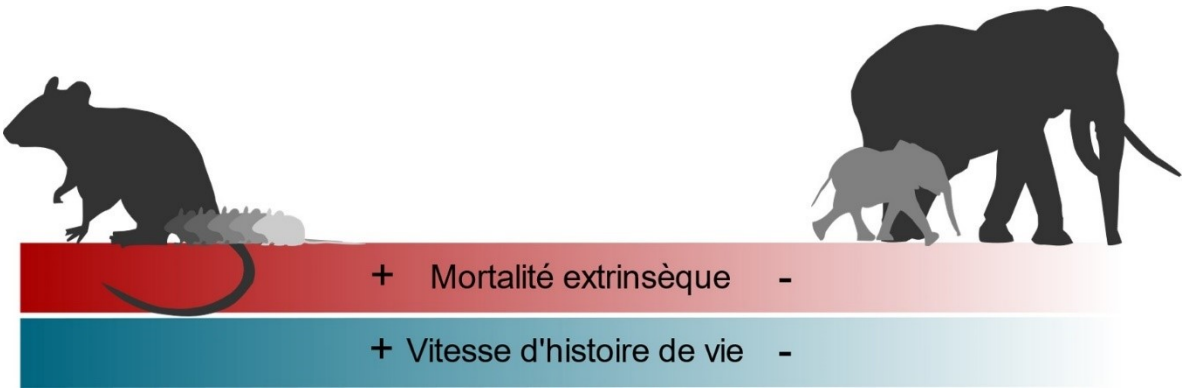

Figure 1.1 Continuum de vitesses d'histoire de vie chez les mammifères.
Le positionnement d'une espèce le long du continuum est déterminé, en partie, par son taux de mortalité extrinsèque. Chez les mammifères, par exemple, les espèces de proies se trouvent à la gauche du continuum et présentent des histoires de vie « rapides » alors que les grandes espèces ayant peu de prédateurs se trouvent à la droite du continuum et présentent des histoires de vie « lentes ».

Le positionnement des espèces le long de ce continuum n'est pas fixe et des déplacements sont possibles si les pressions environnementales changent. Effectivement, une augmentation de la mortalité extrinsèque peut entraîner une accélération des histoires de vie, c'est-à-dire une diminution de l'âge à la première reproduction, une augmentation du nombre et de la fréquence de jeunes produits (p. ex. dans les pêcheries; Law, 2000). Par exemple, les populations de sanglier européen (*Sus scrofa*) sous forte pression de chasse (c.-à-d. forte mortalité extrinsèque) ont des histoires de vie plus rapides; elles présentent des taux de reproduction plus importants que les populations où la chasse est moindre ou interdite (Servanty *et al.*, 2011). De façon similaire, le long historique de persécution des populations européennes d'ours brun pourrait expliquer pourquoi on y trouve des taux de production de jeunes plus élevés relativement à la taille des femelles qu'en Amérique du Nord où la présence de l'Homme est beaucoup plus récente (Zedrosser *et al.*, 2011). Comprendre comment les traits d'histoire de vie sont affectés par les changements environnementaux (p. ex. changements climatiques) permet d'anticiper la persistance ou l'extinction des populations (Paniw *et al.*, 2019).

1.2 Les soins parentaux et leurs coûts et bénéfices

Les soins parentaux incluent tous les comportements des parents susceptibles d'améliorer la valeur adaptative de la progéniture (Clutton-Brock, 1991; Smiseth *et al.*, 2012). Les soins parentaux peuvent prendre diverses formes à travers les espèces et les stades de développement des jeunes. Avant la conception, les soins parentaux incluent les cadeaux nuptiaux et l'apport en nutriments, énergie, anticorps, hormones et antioxydants dans les œufs (Smiseth *et al.*, 2012). Avant la naissance ou l'éclosion des jeunes, le choix de sites, la construction d'un nid ou d'une tanière et le couvage des œufs sont aussi des exemples de comportements parentaux pouvant favoriser la valeur adaptative des jeunes (Clutton-Brock, 1991; Smiseth *et al.*, 2012). Après la naissance ou l'éclosion des jeunes, les principaux soins parentaux incluent la protection (p. ex. contre les prédateurs, ou des parasites), et

l'approvisionnement en nourriture (Clutton-Brock, 1991). Les soins parentaux peuvent aussi se poursuivre au-delà de la période de dépendance nutritionnelle sous la forme de protection, d'apprentissage et d'assistance sociale (p. ex. Hofer et East, 2003).

Bien que les mâles puissent apporter une contribution importante aux soins parentaux chez plusieurs espèces, tels que les insectes, oiseaux et poissons (Clutton-Brock, 1991), les femelles fournissent seules les soins parentaux chez la vaste majorité des espèces animales. On parle alors de soins *maternels* chez ces espèces. Comme le relâchement des gamètes est généralement plus tardif chez les femelles que chez les mâles, les femelles sont contraintes à fournir des soins parentaux lorsque ces derniers sont essentiels à la survie des jeunes (Dawkins et Carlisle, 1976; Kvarnemo, 2010). Chez les mammifères, par exemple, la fertilisation interne et la lactation expliqueraient que les soins parentaux sont prodigués exclusivement par les femelles chez plus de 95 % des espèces (Davies *et al.*, 2012).

Les soins parentaux sont bénéfiques pour la progéniture, mais ils sont coûteux pour les parents. Effectivement, les soins parentaux requièrent du temps et de l'énergie (c.-à-d. un effort parental), ce qui peut se traduire en coûts en valeur adaptative lorsque les ressources sont limitées, soit en une diminution ultérieure du succès reproducteur et de la survie (Trivers, 1972). Par exemple, après une grande allocation d'énergie à la reproduction et aux soins maternels, les femelles peuvent nécessiter une période de récupération avant de se reproduire à nouveau ou produire des jeunes ayant une plus faible probabilité de survie (Balme *et al.*, 2013; Gélin *et al.*, 2015). La sélection naturelle devrait alors favoriser un niveau de soins maternels qui maximise les bénéfices pour la progéniture, tout en minimisant les coûts pour les parents. Un temps viendra donc où les coûts associés à la poursuite des soins maternels surpasseront leurs bénéfices (Trivers, 1974; Davies *et al.*, 2012). À ce stade, les soins maternels devront cesser et les jeunes devront devenir indépendants.

1.3 Variations dans la durée des soins maternels

Le sevrage se traduit par l'atteinte de l'indépendance des jeunes et ne survient que lorsque ces derniers ont atteint un niveau de maturité physique et physiologique suffisant (p. ex. un tractus digestif pleinement fonctionnel et une composition corporelle et efficacité métabolique adéquates) pour leur permettre d'acquérir l'énergie nécessaire pour assurer leur croissance, maintient, survie ainsi que reproduction future (Lee, 1996). Toutefois, il n'existe pas de consensus dans la littérature quant à comment mesurer et déterminer le moment exact du sevrage (Borries *et al.*, 2014). Chez les mammifères, le soin maternel le plus distinctif et le plus énergivore est la lactation (Gittleman et Thompson, 1988). Pour les jeunes, le lait constitue leur première forme de nourriture et représente l'essentiel ou une grande partie de leur alimentation avant l'indépendance. Le sevrage des jeunes chez les mammifères est donc très souvent considéré comme la transition d'une diète principalement constituée de lait vers une diète exempte de lait (Langer, 2003). Cette période de transition peut être plus ou moins longue et se solde soit en la séparation entre les mères et leurs jeunes ou la poursuite des soins maternels sous une autre forme jusqu'à l'atteinte de l'indépendance complète, c.-à-d. l'indépendance nutritionnelle et comportementale des jeunes (Sadleir, 1980; Lavigne et Barrette, 1992; Bădescu *et al.*, 2017). Chez les phocidés et les petits mammifères, le sevrage est abrupt et la dernière tétée (mesurée par la dernière observation directe ou l'absence de traces de lait dans l'estomac ou le sang; Muelbert et Bowen, 1993; Cameron, 1998; Borries *et al.*, 2014) est souvent utilisée comme indicateur du sevrage. Chez les autres espèces de mammifères, le sevrage est plutôt un processus graduel au cours duquel les jeunes transitent lentement vers une diète diversifiée et exempte de lait (Langer, 2003).

L'âge à l'atteinte de l'indépendance, ou la durée des soins maternels, est un trait d'histoire de vie très variable à l'échelle de l'espèce, de la population et de l'individu. Dans une méta-analyse réalisée sur plusieurs espèces de pinnipèdes, d'ongulés et de primates, Lee *et al.*

(1991) montrent qu'il existe une relation étroite entre l'âge et la masse au sevrage et que les jeunes sont sevrés lorsqu'ils atteignent une masse critique correspondant à environ quatre fois leur masse néonatale (Figure 1.2). Les différences interspécifiques dans le développement physiologique et le taux de croissance des jeunes expliqueraient cette relation. Bien que plusieurs groupes taxonomiques en soient exclus, cette méta-analyse suggère néanmoins qu'à travers les espèces, le taux de croissance des jeunes et leur masse au sevrage seraient d'importants déterminants de la durée des soins maternels.

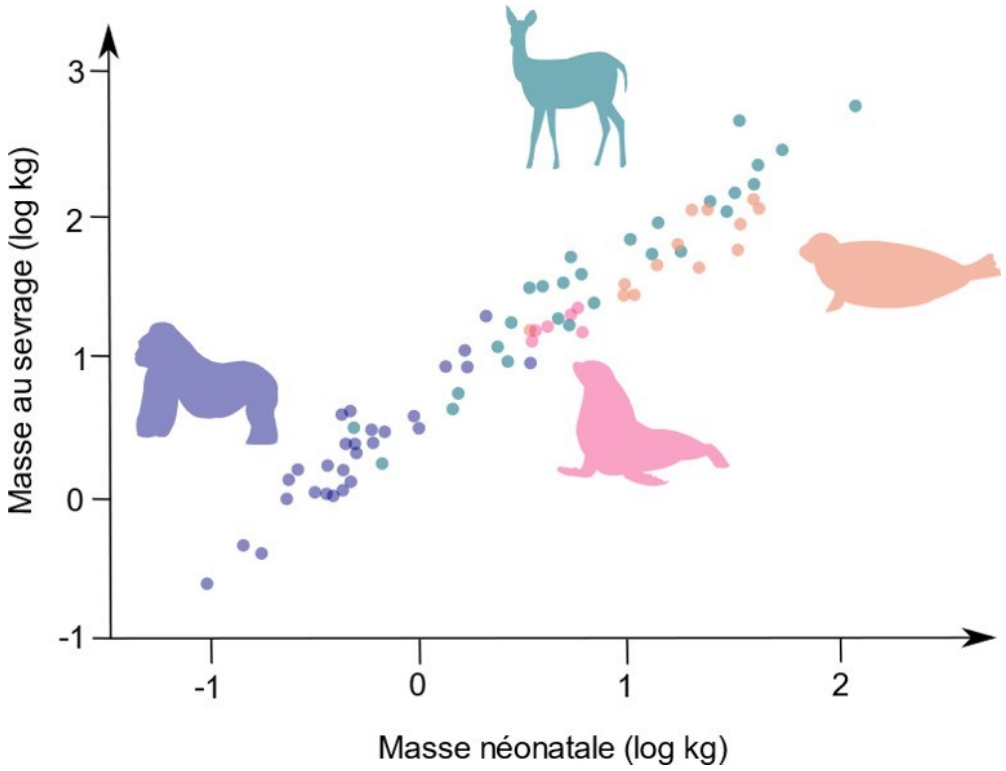

Figure 1.2 **Masse au sevrage des jeunes en fonction de leur masse néonatale à travers plusieurs espèces de primates (violet), d'otaridés (rose), de phocidés (orange) et de cervidés (vert).**

Figure adaptée de Lee *et al.* (1991).

Au niveau intraspécifique, les comparaisons de durée de soins maternels sont principalement réalisées entre les différentes populations d'une même espèce (Lee *et al.*, 1991 ; Borries *et al.*, 2001). Par exemple, chez le Semnopithèque de Cat Ba, *Trachypithecus leucocephalus*, les jeunes sont sevrés environ 13-15 mois plus tard dans les populations sauvages, comparativement aux populations captives avec un accès facilité à la nourriture (Zhao *et al.*, 2008).

Au sein d'une même population, on observe aussi souvent de grandes variations dans la durée des soins maternels entre les individus (Lee, 1996). Par exemple, la lactation peut varier de 35 mois (~2.5 ans) à 96 mois (~8 ans) d'un individu à l'autre chez l'éléphant d'Afrique, *Loxodonta africana*, (Lee et Moss, 1986) et la durée des soins maternels s'étend de 9 à 35 mois chez le léopard d'Afrique, *Panthera pardus* (Balme *et al.*, 2017). Bien qu'elle soit souvent rapportée, peu d'études s'intéressent aux causes de cette variation intraspécifique. Néanmoins, en combinant les résultats des études réalisées sur le sujet, Lee *et al.* (1991) concluent que trois tendances s'en détachent (Figure 1.3).

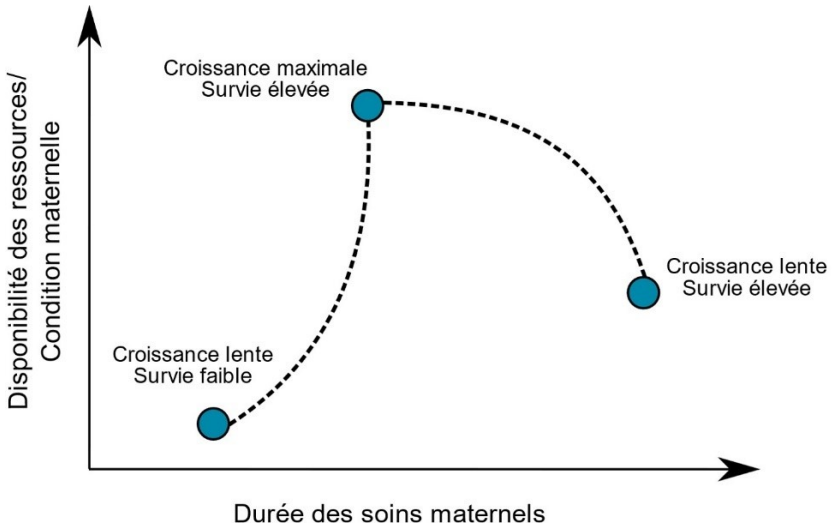

Figure 1.3 Fonction hypothétique (ligne pointillée) reliant la durée des soins (ou âge au sevrage) à la disponibilité de ressources et la condition maternelle.

Les trois scénarios possibles (points) sont présentés dans le texte. Figure adaptée de Lee *et al.* (1991).

Premièrement, dans des environnements peu favorables (p. ex. lorsque les ressources sont peu abondantes), les femelles pourraient terminer les soins maternels de façon prématurée et abandonner leurs jeunes afin de conserver des ressources pour leurs reproductions futures. Les jeunes sevrés prématurément peuvent soit en mourir ou avoir un valeur adaptative réduite, tel qu'observé chez les jeunes mâles mouflons d'Amérique, *Ovis canadensis* (Festa-Bianchet *et al.*, 1994) et le cerf élaphe, *Cervus elaphus* (Andres *et al.*, 2013). Les grands mammifères étant des espèces de type *K*, les femelles devraient prioriser l'investissement dans leur propre survie plutôt que dans l'effort reproducteur lorsque les conditions environnementales sont défavorables et imprévisibles ainsi que lorsque les jeunes sont très sensibles aux variations dans les conditions environnementales (Pianka, 1970 ; Stearns, 1989 ; Festa-Bianchet et Jorgenson, 1998 ; Lindström, 1999). Abandonner les jeunes, dans ce contexte, représente alors une tactique de reproduction efficace si elle

permet aux femelles d'augmenter leur succès reproducteur futur (Tait, 1980). Deuxièmement, un sevrage hâtif peut également s'observer lorsque les ressources sont abondantes. Effectivement, les femelles étant en bonne condition corporelle, elles parviennent à transférer de l'énergie assez efficacement pour que leurs jeunes gagnent de la masse et atteignent rapidement la masse critique pour le sevrage (Lee *et al.*, 1991). Une telle tactique permet d'augmenter le succès reproducteur à vie puisqu'il procure à la fois le bénéfice en valeur adaptative associé à la reproduction actuelle et une reprise rapide des activités de reproduction (Fairbanks et McGuire, 1995). Troisièmement, lorsque la disponibilité des ressources est réduite ou lorsque les conditions environnementales sont moins favorables, acquérir suffisamment d'énergie pour que les jeunes aient une croissance optimale peut représenter un défi pour les femelles. Dans ce contexte, les femelles pourraient prolonger les soins maternels jusqu'à ce que les jeunes atteignent une masse critique avant le sevrage si leurs chances de survie sont bonnes (Trillmich, 1986 ; 1990; Lee et Moss, 1986 ; Lee *et al.*, 1991). En bref, la condition corporelle des mères et des jeunes semble avoir un rôle central dans la détermination de la durée des soins maternels, mais peu d'études ont montré le lien de causalité les unissant (sujet du chapitre 3).

1.4 L'importance du contexte environnemental

La durée des soins maternels dépend aussi de la particularité du contexte environnemental dans lequel les individus vivent. Par exemple, dans les environnements saisonniers, les femelles pourraient ajuster la durée des soins maternels afin d'assurer le *timing* des évènements de reproduction avec les saisons et la disponibilité de la nourriture. Chez plusieurs espèces d'oiseaux, les parents ont plus de chances de se reproduire à nouveau au cours d'une saison en réduisant la période de soins parentaux (Grüebler et Naef-Daenzer, 2008a; Tarwater et Brawn, 2010), et la durée des soins parentaux peut être ajustée en fonction de la disponibilité des ressources pour favoriser les probabilités de survie des jeunes (Grüebler et Naef-Daenzer, 2008b). Chez le léopard d'Afrique, la période de soins

maternels est prolongée lorsque la densité d'impalas, *Aepyceros melampus,* (la principale proie de l'espèce) est faible, ce qui augmente la probabilité de survie des léopardeaux (Balme *et al.*, 2017). Aussi, il peut exister une hétérogénéité individuelle dans l'accès aux ressources, notamment chez les espèces avec une hiérarchie sociale. Par exemple, chez l'hyène tachetée, *Crocuta crocuta*, les femelles à haut rang social ont un accès privilégié aux carcasses, ce qui leur permet de fournir davantage de soins et d'améliorer les chances de survie de leurs jeunes (Hofer et East, 2003). Cette meilleure accessibilité aux ressources pour les femelles occupant un haut rang social permettrait d'écourter la période de soins maternels chez les chimpanzés, *Pan troglodytes* spp. (Lonsdorf *et al.*, 2019). Il est donc important de considérer le contexte dans lequel les animaux vivent pour mieux comprendre leurs tactiques de reproduction et leurs coûts et bénéfices associés.

1.4.1 Conflits sexuels

Le contexte social, du point de vue des interactions entre mâles et femelles, est un autre élément important à considérer dans l'évaluation des déterminants de la durée des soins maternels, bien qu'il soit généralement ignoré. Les conflits sexuels se définissent par des conflits entre les intérêts évolutifs des deux sexes (Parker, 1979). Ils se manifestent par l'expression d'un phénotype comportemental favorisant les intérêts d'un sexe au détriment des intérêts de l'autre sexe (Arnqvist et Rowe, 2005; Trivers, 1972). Les différentes stratégies de reproduction entre les sexes entraînent la sélection pour des comportements et des adaptations morphologiques antagonistes (Arnqvist et Rowe, 2005). Par exemple, chez la plupart des espèces polygynes, les mâles désertent les femelles après l'accouplement, ce qui leur permet d'acquérir des opportunités de reproduction additionnelles et ainsi améliorer leur valeur adaptative (Kokko et Jennions, 2008). Toutefois, ce comportement des mâles force les femelles à rester auprès des jeunes dépendants et à assumer seules les coûts des soins (Trivers, 1972; Clutton-Brock, 1991).

La durée optimale de soins maternels n'est potentiellement pas égale du point de vue des mâles et des femelles. Effectivement, puisque les femelles ne se reproduisent à nouveau qu'après le sevrage des jeunes actuels chez plusieurs espèces de mammifères (Lee et Moss, 1986; Steyaert *et al.*, 2012; Balme *et al.*, 2017), de longs soins maternels diminuent les probabilités d'accouplement pour les mâles. Pour augmenter leurs succès reproducteurs, les mâles auraient alors intérêt à raccourcir la période de soins maternels (Lessels, 1999). La fin des soins maternels a effectivement été associée à la présence de mâles et d'interactions agressives chez certains mammifères, tels que les primates et les carnivores (Dahle et Swenson, 2003b; Zhao *et al.*, 2011; Morino et Borries, 2017). On sait que les femelles peuvent adopter des contre-stratégies face aux comportements des mâles (Agrell *et al.*, 1998), mais on en connaît très peu sur la dynamique entre les mâles et les femelles au moment de la séparation des groupes familiaux et sur le rôle joué par les mâles dans la fin des soins maternels. Ce sujet est abordé au chapitre 4.

1.4.2 Pressions sélectives induites par l'Homme et ses activités

Les traits phénotypiques peuvent changer au cours du temps via les flux de gènes, la dérive génétique, les mutations, la plasticité phénotypique et la sélection (Hendry et Kinnison, 1999). Alors que les flux de gènes, la dérive génétique et les mutations représentent des processus évolutifs neutres, les changements phénotypiques résultant de la plasticité phénotypique et de la sélection impliquent une réponse à un signal ou à un changement environnemental particulier (Gienapp *et al.*, 2008). La plasticité phénotypique se définit par l'expression de phénotypes différents dans différents environnements par un même génotype et n'implique donc pas de changements génétiques (DeWitt et Schneider, 2004). L'évolution par sélection, quant à elle, réfère à des changements génétiques résultant des différences en reproduction des individus dans de nouveaux environnements (Gienapp *et al.*, 2008; Fox et Westneat, 2010). Les changements d'ordre plastiques ou génétiques peuvent être adaptatifs, ou non. Par exemple, la dérive génétique est un processus aléatoire,

non-adaptatif, entraînant des changements génétiques dans la population (Merilä et Hendry, 2014). Les changements adaptatifs, quant à eux, résultent d'un changement phénotypique survenant en réponse à un signal environnemental se traduisant par une amélioration de la croissance, de la survie et de la reproduction des individus (Stearns, 1992).

Alors qu'on croyait que l'évolution n'était qu'un processus lent (Darwin, 1859), on constate maintenant que l'évolution peut s'observer à l'échelle de quelques générations seulement (Merilä *et al.*, 2001). On parle alors de micro-évolution ou d'évolution contemporaine. Toutefois, pour observer l'évolution par sélection naturelle, trois conditions sont requises : il doit y avoir de la diversité phénotypique entre les individus d'une même population (variabilité), la valeur adaptative des individus doit différer en fonction des phénotypes qu'ils expriment (sélection), et les différents phénotypes doivent être issus de génotypes différents (héritabilité; Darwin, 1859). Dans les populations sauvages, la sélection naturelle est le mécanisme par lequel les organismes peuvent s'adapter à long-terme aux changements dans les conditions environnementales. Le principe de la sélection est simple : les individus exprimant des phénotypes héritables leur procurant une meilleure survie et un meilleur succès de reproduction auront plus de descendants (Freeman et Herron, 2007). Un exemple classique est celui des phalènes du bouleau, *Biston betularia*, en Grande-Bretagne qui ont changé de coloration suite à la révolution industrielle qui a noirci l'écorce des arbres. Les individus présentant une coloration plus foncée étaient mieux camouflés et évitaient davantage la prédation que les individus à coloration plus claire (Majerus, 2009).

Les changements évolutifs contemporains sont toutefois difficiles à montrer en nature, en partie dû à des fluctuations temporelles dans la direction de la sélection (Merilä *et al.*, 2001). Cependant, si la pression de sélection est forte et constante, comme dans le cas de l'exploitation par l'Homme, et qu'elle affecte des traits héritables, l'évolution contemporaine peut être observée (Hendry et Kinnison, 1999; Darimont *et al.*, 2009; van

Wijk *et al.*, 2013; Pigeon *et al.*, 2016). Bien qu'il existe un grand intérêt actuellement pour montrer l'évolution contemporaine, la sélection à elle seule peut entraîner des conséquences démographiques importantes méritant notre attention (Law, 2000).

1.4.3 Effets directs et indirects de la chasse dans les populations animales sauvages

À l'ère de l'Anthropocène, l'omniprésence de l'Homme et de ses activités représente la plus grande menace à la biodiversité (Pelletier et Coltman, 2018). Face à cette menace grandissante, les populations animales sauvages peuvent soit s'éteindre, se déplacer, ou s'adapter par plasticité phénotypique ou évolution. La surexploitation a mené plusieurs espèces au gouffre de l'extinction et plusieurs populations animales sauvages sont actuellement menacées par cette pression anthropique (Lambert, 2013; Pelletier et Coltman, 2018). Les populations animales qui persistent dans des environnements dominés par l'Homme présentent souvent des traits comportementaux particuliers leur permettant d'en tirer profit (Bateman et Fleming, 2012). Le dérangement et la prédation par l'Homme sont actuellement les plus importantes forces sélectives à l'œuvre (Darimont *et al.*, 2009), entraînant des changements dans les traits comportementaux, mais aussi dans les traits morphologiques et d'histoire de vie.

Beaucoup de populations animales sont actuellement exploitées, ou l'ont été par le passé, pour des raisons économiques, sportives et/ou de gestion. La conséquence directe la plus évidente de l'exploitation, ou du fait de récolter des individus d'une population, est la diminution de la survie, par conséquent, du taux de croissance de la population. On reconnaît de plus en plus que la récolte peut entraîner une vaste gamme de conséquences indirectes (et souvent non-intentionnelles) sur les traits phénotypiques et la dynamique de population (Law, 2000; Harris *et al.*, 2002; Fenberg et Roy, 2008; Darimont *et al.*, 2009; Allendorf et Hard, 2009; Mysterud, 2011; Frank *et al.*, 2017). Par exemple, une diminution

de la densité de la population due à la récolte allège la compétition intraspécifique, ce qui a pour conséquence d'accélérer la croissance et l'atteinte de la maturité sexuelle pour les individus survivants (Law, 2000).

La récolte peut induire des pressions de sélection sur les populations animales sauvages de façon intentionnelle ou non (Bunnefeld *et al.*, 2009). Lorsqu'aléatoire, la récolte augmente la mortalité extrinsèque d'une population, ce qui peut entraîner une accélération dans la vitesse d'histoire de vie d'une population en sélectionnant pour un plus grand investissement dans la reproduction (Heino *et al.*, 2015). Toutefois, la récolte est généralement non-aléatoire dû à des préférences de la part des humains, des différences individuelles dans la vulnérabilité des animaux ainsi que le type de récolte et sa réglementation qui ciblent certains phénotypes en particulier (Harris *et al.*, 2002; Festa-Bianchet, 2003; Fenberg et Roy, 2008; Mysterud, 2011). Le caractère non-aléatoire de la chasse a pour conséquence que certains individus possédant des phénotypes particuliers seront retirés de la population de façon disproportionnée par rapport aux autres, ce qui induit une pression de sélection favorisant les phénotypes non ciblés. Bien que les évidences de la sélection induite par la chasse concernent à ce jour surtout les traits morphologiques, la chasse peut aussi induire des pressions de sélection sur les traits comportementaux (Ciuti *et al.*, 2012; Leclerc *et al.*, 2017b; 2019), et les traits d'histoire de vie (Festa-Bianchet, 2003; Rughetti et Festa-Bianchet, 2014).

Les chasseurs montrent généralement des préférences pour certaines valeurs de traits phénotypiques lorsqu'ils en ont l'opportunité (Mysterud, 2011). Dans le cadre de la chasse au trophée, par exemple, les chasseurs sportifs sont enclins à débourser d'importantes sommes d'argent pour récolter les individus possédant les plus grands attributs (p. ex. cornes, bois ou défenses), ce qui réduit artificiellement la survie de ces derniers (Coltman *et al.*, 2003; Pigeon *et al.*, 2016). De plus, chez les ongulés et les carnivores, la chasse

sélective peut affecter la structure d'âge et de sexe d'une population avec des conséquences démographiques (Milner *et al.*, 2007).

Des effets sélectifs et démographiques sont aussi attendus lorsque les chasseurs évitent activement de tuer certaines classes d'individus pour des raisons éthiques ou légales. Effectivement, une réglementation fréquemment observée pour assurer une exploitation durable est la protection des femelles adultes, puisque ce sont ces dernières qui contribuent le plus à la croissance d'une population (Caswell, 2001). Chez les espèces où il est difficile de différencier les mâles des femelles solitaires à distance (p. ex. chez l'ours brun; Bischof *et al.*, 2008), la protection des femelles accompagnées de jeunes dépendants peut servir de moyen alternatif pour éviter que les chasseurs ne tuent des femelles (Miller, 1990). Même dans les systèmes où la réglementation ne l'interdit pas, les chasseurs peuvent montrer des réticences éthiques à tuer des membres de groupes familiaux, principalement face à la perception que les jeunes orphelins ont une plus faible probabilité de survie (Bischof *et al.*, 2009; Krofel *et al.*, 2012; Rughetti et Festa-Bianchet, 2014). Par exemple, chez le chamois alpin, *Rupicapra rupicapra*, les chasseurs tuent préférentiellement des femelles non-lactantes (Rughetti et Festa-Bianchet, 2011). La principale conséquence de cette réglementation, ou de cet évitement, est un biais de récolte vers les mâles et les femelles non-reproductrices (Solberg *et al.*, 2000; Bischof *et al.*, 2009; Rughetti et Festa-Bianchet, 2011). Par exemple, en Slovénie, où il est interdit de tuer des femelles ours brun accompagnées de jeunes dépendants, on observe que, contrairement aux autres causes de mortalité, la mortalité à la chasse est biaisée vers les mâles (Krofel *et al.*, 2012). En Norvège, la réticence des chasseurs à tuer des femelles orignaux, *Alces alces*, accompagnées de veaux augmente la récolte de femelles des groupes d'âge moins productifs (Solberg *et al.*, 2000). En se basant sur des simulations, Rughetti et Festa-Bianchet (2014) ont montré que l'évitement par les chasseurs des femelles lactantes peut affecter la mortalité âge-spécifique, la structure d'âge et la dynamique d'une population et ce, de façon plus prononcée à forte intensité de chasse. Bien que ce type de sélection induite par la chasse semble omniprésent au sein des populations animales chassées, peu

d'études l'ont montré empiriquement et encore moins d'études en ont montré les conséquences démographiques. Ce sujet est abordé au chapitre 5.

1.5 Conséquences individuelles et populationnelles de la variation en durée de soins maternels

Peu importe ses causes, la variation dans la durée des soins maternels peut entraîner des conséquences individuelles et démographiques. Puisque les femelles de plusieurs espèces ne se reproduisent à nouveau que lorsqu'elles ont sevré leurs jeunes actuels (Quesnel et Prunier, 1995), l'intervalle de temps entre deux conceptions, ou naissances (Borries *et al.*, 2001), une composante importante du succès reproducteur à vie, est donc intimement lié à la durée des soins maternels. De plus longs soins maternels signifient que la prochaine reproduction sera retardée et que le temps total disponible pour des reproductions futures sera réduit (Trillmich, 1990; Tarwater et Brawn, 2010; Balme *et al.*, 2017). Effectivement, chez le léopard d'Afrique, procurer des soins maternels courts, plutôt que longs, peut augmenter jusqu'à 25 % le succès reproducteur à vie des femelles (Balme *et al.*, 2017). La variation dans la durée des soins maternels peut donc avoir des conséquences importantes sur la valeur adaptative des femelles. Toutefois, les coûts en pertes d'opportunité en reproduction peuvent être compensés par une augmentation de la valeur adaptative inclusive (Hamilton, 1964) si une prolongation des soins maternels apporte des gains en survie à la progéniture (Balme *et al.*, 2017).

1.5.1 Dynamique de population et soins maternels

Puisque la durée des soins maternels a le potentiel d'influencer les taux de survie et de reproduction individuels, un changement dans ce trait d'histoire de vie peut aussi avoir des

conséquences démographiques qui peuvent être mesurées par une approche de dynamique de population. Le taux de croissance d'une population est un concept central en écologie des populations (Sibly et Hone, 2002), permettant d'évaluer si une population est stable ou si, et à quel rythme, elle croît ou décline. Le taux de croissance d'une population est généralement représenté par λ, soit le taux de croissance asymptotique d'une population (Caswell, 2001). Il correspond au taux *per capita* d'augmentation de la population dans un intervalle de temps donné, habituellement une année (Sibly et Hone, 2002). Une population est en croissance lorsque $\lambda > 1$ et en décroissance lorsque $\lambda < 1$, alors qu'elle est considérée stable lorsque $\lambda = 1$. Le modèle de croissance de population le plus simple est le modèle exponentiel;

$$N_{t+1} = \lambda N_t \qquad \text{(équation 1.1)}$$

où N_t est la taille de population au temps t et N_{t+1} est la taille de population au temps $t+1$. Des modèles plus complexes, incorporant de la densité-dépendance et de la stochasticité environnementale (p. ex. prédation, compétition interspécifique, fluctuations en ressources alimentaires) offrent toutefois un meilleur portrait de la réalité (Sinclair et Pech, 1996; Saether, 1997; Bieber et Ruf, 2005). Pour identifier les déterminants du taux de croissance d'une population, on s'intéresse aux liens directs entre la dynamique de population et les facteurs externes, tels que les fluctuations climatiques, la compétition, la prédation, le parasitisme et les fluctuations dans les ressources (approche mécanistique; voir Turchin, 1999), ou aux relations entre le taux de croissance et les paramètres démographiques de survie et de reproduction (approche démographique; p. ex. Seamans *et al.*, 1999) ou encore à une combinaison de ces approches (Hunter *et al.*, 2010).

Les modèles démographiques sont utiles pour estimer le taux de croissance d'une population et faire des projections quant aux trajectoires populationnelles futures. Dans les populations fermées (c.-à-d. absence d'émigration et d'immigration), le taux de croissance est gouverné par les taux de reproduction et de survie (Caswell, 2001; Coulson et Godfray,

2007). Dans les modèles de population, les individus transitent au sein d'un cycle de vie selon des probabilités de transitions données par les taux de survie et de reproduction. Puisque ces taux sont généralement âge-dépendants (Coulson et Godfray, 2007; Pelletier *et al.*, 2011), les modèles de population et leur représentation sous forme de cycle de vie sont généralement structurés en âge (Caswell, 2001). Un exemple de cycle de vie est donné à la Figure 1.4.

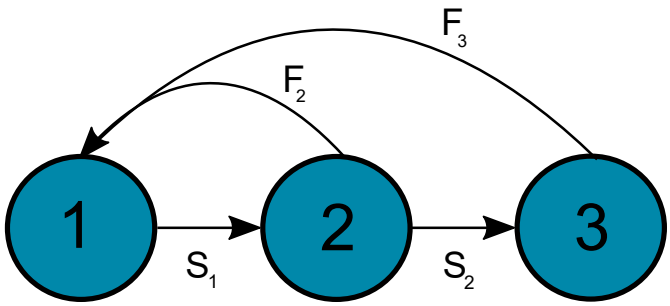

Figure 1.4 **Exemple d'un cycle de vie.**

Cet exemple, simple, représente une population fictive comprenant 3 classes d'âge (cercles) et quatre probabilités de transition (flèches) d'une année à l'autre entre ces classes d'âge données par les taux de survie S_1 et S_2 (tous les individus de 3 ans meurent l'année suivante). Les individus des classes d'âge 2 et 3 peuvent contribuer à la classe d'âge 1 l'année suivante via leur taux de fécondité (c.-à-d. la probabilité de survivre et de se reproduire l'année suivante); F_2 et F_3.

Au sein d'une classe d'âge donnée, les taux démographiques peuvent être fixes ou varier stochastiquement et en fonction de la densité-dépendance (Saether, 1997; Otto et Day, 2007). Les modèles les plus simples de dynamique de population sont déterministes (c.-à-d.

taux démographiques fixes), n'incluent que la composante femelle de la population et considèrent la population comme fermée (Eberhardt, 2002). Le cycle de vie d'une population peut être traduit en une matrice, c.-à-d. une matrice de Leslie **A**, qui, multipliée par le vecteur initial de taille de population pour chaque classe d'âge ($\mathbf{n}_t = (n_1, n_2, n_3)_t$), permet d'estimer le nombre d'individus dans chaque classe d'âge à un pas de temps ultérieur. En utilisant le cycle de vie de la figure 1.4 et la matrice **A** qui en découle;

$$\boldsymbol{n}_{t+1} = \begin{pmatrix} 0 & F_2 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & 0 \end{pmatrix} \boldsymbol{n}_t \qquad \text{(équation 1.2)}$$

En se basant sur les propriétés matricielles, les matrices de Leslie permettent d'extraire des informations très pertinentes en dynamique de population. Effectivement, il est possible ainsi d'extraire la valeur propre dominante de **A**, qui correspond au taux de croissance asymptotique (λ) de la population et d'autres métriques, telles que la distribution d'âge à l'équilibre ($\boldsymbol{w}$), ainsi que la valeur reproductive de chaque classe d'âge ($\boldsymbol{v}$) et le temps de génération (T) de la population (Caswell, 2001).

La durée des soins maternels (et sa variation) a le potentiel d'influencer les taux de reproduction et de survie populationnels et, ultimement, la dynamique d'une population. Par exemple, chez l'ours brun scandinave, l'intervalle entre les naissances est déterminé principalement par la durée des soins maternels et explique 79 % de la variation dans le taux de reproduction de la population (Swenson et Sandegren, 1999). Une augmentation de la durée des soins maternels à l'échelle de la population pourrait donc entraîner une diminution du taux de reproduction dans cette population. Durant la période d'association mère-jeunes, la survie des jeunes est principalement dépendante des soins maternels et les jeunes bénéficient d'un apport en nourriture et d'une protection de la part de leurs mères (Clutton-Brock, 1991), ce qui augmente leur probabilité de survie. Par exemple, la probabilité d'abandon des jeunes est élevée lorsque les conditions environnementales sont

défavorables, ce qui réduit la survie des jeunes à l'échelle de la population. Chez l'otarie à fourrure des îles Galapagos, *Zalophus californianus wollebaeki*, la plupart des chiots ont été abandonnés et sont morts de faim suite à l'effondrement de la productivité primaire et secondaire durant l'épisode *El niño* de 1983 (Trillmich et Limberger, 1985). Au sevrage, la survie des jeunes est principalement affectée par des facteurs indépendants des soins maternels, tels que la densité de la population, les conditions climatiques difficiles, la prédation et les maladies (Gaillard *et al.*, 2000). Les jeunes classes d'âges ont souvent les plus faibles taux de survie et sont les plus vulnérables aux fluctuations environnementales (Gaillard *et al.*, 2000). En retardant l'âge à l'indépendance et donc en diminuant la période de vulnérabilité des jeunes, de plus longs soins maternels peuvent augmenter le taux de survie de cette classe d'âge (Balme *et al.*, 2017). Les femelles adultes, quant à elles, ont généralement des taux de survie très élevés et peu variables chez les grands mammifères en raison de la canalisation de la sélection vers la survie chez les espèces de type *K* (Stearns, 1992; Gaillard *et al.*, 2000). Toutefois, des changements dans la survie adulte ont le plus grand potentiel d'influencer le taux de croissance de la population (Sæther *et al.*, 2013). Des soins maternels plus longs, s'ils entraînent un coût en survie individuelle, peuvent diminuer le taux populationnel de survie des femelles adultes. De plus, bien que la courbe de mortalité âge-spécifique suit généralement un patron en forme d'un *U* dans les populations naturelles (Gaillard *et al.*, 1998), ce patron peut être renversé au sein des populations exploitées où la mortalité induite par l'Homme peut aussi affecter les femelles adultes (Bischof *et al.*, 2018) avec des conséquences importantes sur le taux de croissance d'une population. Toutefois, des soins maternels longs pourraient augmenter les probabilités de survie des femelles dans les populations chassées où la réglementation de la chasse interdit de tuer des femelles avec des jeunes dépendants. Évaluer les conséquences démographiques de la variation dans la durée des soins maternels requiert donc de soupeser les coûts et bénéfices en survie et reproduction associés dans le contexte particulier où vivent les individus, tel qu'une chasse intensive.

1.6 Objectifs

Cette thèse vise principalement à mieux comprendre les tactiques de reproduction maternelles et l'influence du contexte environnemental sur celles-ci. Plus précisément, elle vise à identifier les déterminants de la durée des soins maternels et l'évaluation des conséquences individuelles et populationnelles de la variation dans ce trait d'histoire de vie chez l'ours brun scandinave. Cette thèse se décompose en quatre sous-objectifs distincts :

1) Intégrer l'hétérogénéité phénotypique au sein des portées dans l'évaluation des tactiques d'allocation maternelle dans le contexte du compromis d'histoire de vie entre la masse et le nombre de jeunes produits (chapitre 2);

2) Mesurer et contraster la contribution relative de la masse des jeunes et de ses déterminants à la variation dans la durée des soins maternels dans différents contextes environnementaux (chapitre 3);

3) Explorer le rôle du contexte de conflits sexuels dans les tactiques de reproduction et la durée des soins maternels (chapitre 4);

4) Évaluer le potentiel sélectif de la chasse et de sa réglementation sur la durée des soins maternels et estimer ses conséquences individuelles et démographiques (chapitre 5)

Pour rencontrer les objectifs visés par cette thèse, j'ai eu le privilège d'accéder aux données récoltées depuis près de 30 ans sur la population suédoise d'ours brun via le Scandinavian Brown Bear Research Project (SBBRP). J'ai utilisé de l'information détaillée sur les traits d'histoire de vie des femelles ours, souvent de leur naissance jusqu'à leur mort, incluant des informations sur leurs oursons (nombre, masse), leurs localisations géographiques (c.-à-d. localisations GPS) et les récoltes à la chasse. Peu de systèmes d'études permettent à la fois de combiner un étoffé suivi à long-terme d'animaux sauvages individuellement

marqués et des registres de chasse bien documentés. Grâce à ces données, j'ai répondu à des questions sur lesquelles peu de chercheurs ont pu se pencher jusqu'à présent.

1.7 Méthodes

1.7.1 Espèce à l'étude

L'ours brun, une des huit espèces d'ours et un des six membres du genre *Ursus* a une distribution holarctique et on le retrouve à travers l'Europe, l'Asie et l'Amérique du Nord (Schwartz *et al.*, 2003). En Amérique du Nord, l'ours brun est plus communément appelé « ours grizzly ». On retrouve l'ours brun dans un large éventail d'environnements, allant de la toundra arctique aux régions montagneuses, en passant par les forêts côtières. Étant un omnivore opportuniste, son régime alimentaire varie grandement d'une saison et d'une population à l'autre en fonction de la disponibilité locale et saisonnière des ressources alimentaires (Schwartz *et al.*, 2003). Les principaux éléments constituant la diète de l'ours brun sont les baies, l'herbe, les racines, les bulbes et les noix, les insectes et les vertébrés (poissons, mammifères et oiseaux consommés soit par prédation ou charognage). L'abondance et la disponibilité de nourriture de haute qualité détermine la taille corporelle, les taux de reproduction et la densité d'individus à travers les populations d'ours brun (Hilderbrand *et al.*, 1999).

Chez l'ours brun, la taille corporelle et la masse des individus varient en fonction de la localisation géographique et de la saison ainsi que du sexe et de l'âge des individus. Le dimorphisme sexuel est grand puisque les mâles ont une taille environ 1,2 à 2,2 fois supérieure à celle des femelles (Hilderbrand *et al.*, 1999; Schwartz *et al.*, 2003; Swenson *et al.*, 2007). Les femelles atteignent 90 % de leur taille asymptotique vers l'âge de 4,1 à 4,7

ans en Scandinavie (Zedrosser *et al.*, 2006) et leur masse varie entre 108-156 kg en Amérique du Nord et entre 94-142 kg en Europe (Zedrosser *et al.*, 2011). Afin de pallier les conditions hivernales extrêmes, l'ours brun a développé des adaptations physiologiques et comportementales lui permettant de réduire son métabolisme d'environ 70 % durant l'hibernation et de passer jusqu'à 7 mois sans se nourrir, déféquer ou uriner (Manchi et Swenson, 2005). Les variations saisonnières en masse sont très importantes chez cette espèce avec une importante accumulation de réserves adipeuses durant la période active afin de survivre à la période d'hibernation où les individus peuvent perdre jusqu'à 32 % de leur masse corporelle (Schwartz *et al.*, 2003).

L'ours brun est une espèce solitaire et non-territoriale; les individus occupent des domaines vitaux plutôt que des territoires stricts (Craighead *et al.*, 1995; Dahle et Swenson, 2003a). Les mâles occupent des domaines vitaux très larges (>800 km^2) qui incluent plusieurs domaines vitaux femelles (Dahle et Swenson, 2003a; Frank *et al.*, 2018). Durant la saison de reproduction, qui s'étale sur 2,5 mois de la fin du printemps jusqu'au début de l'été (Craighead *et al.*, 1995; Dahle et Swenson, 2003b), les mâles et les femelles étendent leurs domaines vitaux afin de favoriser les interactions avec les membres du sexe opposé (Dahle et Swenson, 2003a). Le système d'appariement de l'espèce est la polygamie, c.-à-d. que plusieurs mâles s'accouplent avec plusieurs femelles, et vice-versa (Steyaert *et al.*, 2012).

La gestation, la parturition ainsi que le début de la lactation ont lieu durant l'hibernation. La gestation est très courte (56 jours; Friebe *et al.*, 2014), ce qui limite les coûts énergétiques liés à la reproduction. En tronquant la durée de la période de développement embryonnaire, la taille des jeunes à la naissance est réduite, ce qui diminue les coûts initiaux de la lactation (Spady *et al.*, 2007). Les femelles donnent naissance, en tanière, en janvier (Friebe *et al.*, 2014) à un à quatre oursons, mais le mode est de deux oursons (Pasitschniak-Arts, 1993; Schwartz *et al.*, 2003). Les oursons ne pèsent qu'environ 0,5 kg à la naissance et sont aveugles et complètement dépendants (Pasitschniak-Arts, 1993). Les soins maternels

incluent la thermorégulation, l'approvisionnement en nourriture sous forme de lait, l'accès à des ressources alimentaires, l'apprentissage et la protection (Schwartz *et al.*, 2003). On en connaît très peu sur le comportement d'allaitement et l'énergétique de la lactation en milieu naturel. Toutefois, selon les observations d'ours brun en captivité, la consommation de lait des oursons débute en tanière et atteindrait un sommet à la mi-été pour ensuite diminuer après 150 jours alors que les oursons commencent à se nourrir d'autres sources alimentaires (Farley et Robbins, 1995). Puisque les soins maternels se poursuivent après l'allaitement, on parle alors de durée de soins maternels plutôt que de d'âge au sevrage chez l'ours brun.

La vitesse et les traits d'histoire de vie (p. ex. taille de portée, âge à la première reproduction) varient entre les populations d'ours brun à travers le monde (Nawaz *et al.*, 2008). Les oursons restent avec leur mère de 1,5 à 4,5 ans, dépendant des populations. En effet, la durée des soins maternels est généralement plus courte dans les populations européennes que nord-américaines; les groupes familiaux se séparent plus souvent après 1,5 ans en Europe *vs* 2,5 ans en Amérique du Nord (Swenson *et al.*, 1994; Schwartz *et al.*, 2003). La période de séparation des groupes familiaux survient avant la période d'accouplements, mais ces deux périodes montrent un large chevauchement (Dahle et Swenson, 2003b). Chez l'ours brun, la lactation supprime l'œstrus (Steyaert *et al.*, 2012). Ainsi, la durée des soins maternels influence l'intervalle entre les naissances et de plus longs soins maternels signifient un coût reproducteur, c'est-à-dire une diminution d'opportunités de reproduction futures.

1.7.2 L'ours brun en Scandinavie

En Scandinavie, la durée des soins maternels est soit de 1,5 (soins couts) ou 2,5 ans (soins longs). Les groupes familiaux se séparent au printemps et les oursons d'un même groupe familial se séparent au cours d'une même semaine (Dahle et Swenson, 2003b). En se basant

sur 29 portées au nord de la Suède, (Dahle et Swenson, 2003c) ont montré que la durée des soins maternels était influencée par la masse des oursons à l'âge d'un an; les portées avec des plus petits oursons restaient avec leur mère une année supplémentaire. Une plus longue durée de soins maternels est avantageuse pour les oursons puisqu'ils ont un meilleur taux de croissance et de survie que les oursons n'ayant reçu que 1,5 ans de soins maternels (Dahle et Swenson, 2003c; Zedrosser *et al.*, 2013).

Le long intervalle de temps entre les naissances chez l'ours brun est source de conflits sexuels et les mâles exhibent des comportements leur permettant de raccourcir cet intervalle. L'Infanticide Sexuellement Sélectionné, ISS, c.à.d. la mortalité des jeunes dépendants causée par un mâle qui n'est pas le père afin de gagner une opportunité de reproduction avec la femelle (Hrdy, 1979), est un comportement des mâles fréquemment observé en Scandinavie (Swenson *et al.*, 2001). La majorité (85 %) des mortalités d'oursons de l'année survient au printemps alors que la probabilité de survie des oursons n'est que de 63 % (Gosselin *et al.*, 2017). L'ISS expliquerait 15 % des changements dans le taux de croissance de la population (Gosselin *et al.*, 2015). Ce comportement, s'observant durant la période de reproduction (Gosselin *et al.*, 2017), est efficace puisque les femelles retournent en œstrus rapidement après avoir perdu leurs oursons (Steyaert *et al.*, 2014). De façon similaire, dans la plupart des cas de séparation de groupes familiaux observés, des mâles se trouvaient à proximité, ce qui suggère leur rôle potentiel dans la fin des soins maternels (Dahle et Swenson, 2003b). Pour éviter les interactions agressives avec les mâles, telles que l'ISS, les femelles peuvent adopter des contre-stratégies (Hrdy, 1979), telles que la paternité multiple pour confondre la paternité et l'évitement des mâles durant la période de reproduction (Bellemain *et al.*, 2006; Steyaert *et al.*, 2013; 2016).

L'Homme et ses activités ont modulé l'abondance, les traits d'histoire de vie et le comportement de l'ours brun en Scandinavie. En 1850, on y trouvait environ 4000-5000 individus (Swenson *et al.*, 1995). À cause de la perte d'habitat, la persécution et la chasse

sur prime, l'ours brun a été pratiquement éliminé en Norvège en 1920, alors que les effectifs de la population ont atteint un creux de 130 individus en 1930 en Suède (Swenson *et al.*, 1995; 2017). À la suite de l'application de mesures de protection en Suède (p. ex. cessation de la chasse sur prime en 1893), l'abondance de la population a augmenté et la chasse a été permise à nouveau en 1943 (Bjärvall, 1990). La population est actuellement toujours en croissance, mais à un rythme ralenti (Swenson *et al.*, 2017). Elle demeure toutefois l'une des plus productives au monde (Saether *et al.*, 1998; Zedrosser *et al.*, 2011) et le fort taux de mortalité extrinsèque du au long historique de persécution passé de l'espèce en Scandinavie, aurait sélectionné pour un taux de reproduction élevé (Zedrosser *et al.*, 2011). La population d'ours brun scandinave se positionne ainsi le plus à gauche du continuum des vitesses d'histoire de vie (Figure 1.1) pour l'espèce.

La chasse représente la plus importante cause de mortalité d'ours en Suède (Bischof *et al.*, 2009). À l'échelle de la Suède, le taux de récolte annuel est d'environ 4,1-5,1 % de la population totale (Kindberg et Swenson, 2006). Toutefois, dans le sud de la Suède, la proportion d'ours marqués disponibles à la chasse qui sont tués annuellement gravite autour de 30 % ces dernières années (Figure 1.5). En plus d'influencer la taille de la population, la chasse entraîne de nombreux effets indirects (revus dans Frank *et al.*, 2017). Effectivement, la chasse et le paysage de la peur qu'elle génère, a été associée à plusieurs changements comportementaux chez cette population (Ordiz *et al.*, 2012; Støen *et al.*, 2015; Hertel *et al.*, 2016). De plus, en retirant des mâles de la population, la chasse force une réorganisation spatiale des domaines vitaux (Leclerc *et al.*, 2017a), augmentant ainsi les risques de rencontre entre les groupes familiaux et de nouveaux mâles et, par conséquent, les conflits sexuels et l'ISS (Gosselin *et al.*, 2017).

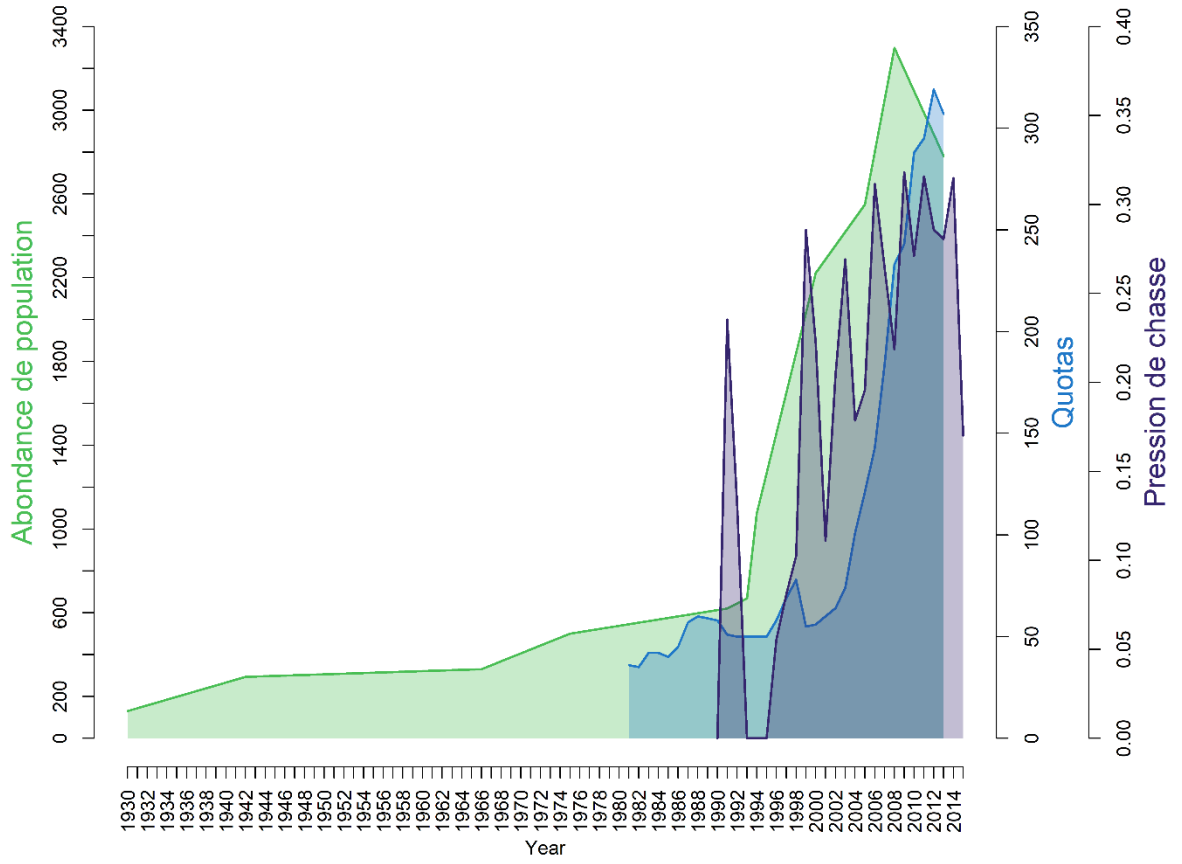

Figure 1.5 **Changements temporels dans l'abondance de le population (vert), les quotas (bleu) et la pression (violet) de chasse de l'ours brun en Suède.** La pression de chasse correspond à la proportion d'ours marqués tués à la chasse par rapport au nombre total d'ours disponibles à la chasse à chaque année. Les données utilisées pour ce graphique sont issues de Swenson *et al.*, (2017) et du suivi d'individus marqués effectué par le SBBRP.

En Suède, la chasse débute à la fin août et s'étend jusqu'à la mi-octobre ou jusqu'à ce que les quotas soient remplis (Bjärvall, 1990). Les objectifs de gestion de la population et, par conséquent, la réglementation de la chasse, ont changé au cours des 30 dernières années (Swenson *et al.*, 2017). Actuellement, les quotas de chasse sont établis annuellement à

l'échelle du comté (Bischof *et al.*, 2008). Les chasseurs n'ont pas besoin de permis de chasse à l'ours, seulement d'un permis de chasse pour un territoire de chasse donné et d'une arme légale conçue pour le gros gibier (Bischof *et al.*, 2008). Tout ours solitaire peut être tué sans égard à son âge ou son sexe, ce qui porte à croire que la chasse est non-sélective (Bischof *et al.*, 2009). Toutefois, depuis 1985, les membres de groupes familiaux (femelles et jeunes dépendants de n'importe quel âge) bénéficient d'un statut de protection légale. Compte tenu de cette réglementation, la chasse est forcément sélective, puisqu'elle cible une portion de la population : les mâles et les femelles non-reproductrices (jeunes femelles et femelles solitaires entre 2 évènements de reproduction). En étant disponibles moins souvent pour la chasse, les femelles procurant des soins maternels longs (2,5 ans) seraient davantage protégées de la chasse et plusieurs ont suggéré que la chasse induirait une sélection pour des soins maternels plus longs dans la population (Zedrosser *et al.*, 2013; Bischof *et al.*, 2018).

1.8 Aire d'étude

Le suivi de la population d'ours brun en Suède est réalisé par le SBBRP dans deux aires d'études séparées par 600 km (Figure 1.6); le nord (comté de Norrbotten) et le sud (comtés de Dalarna et Gävleborg). Le site d'étude au nord (localisation approximative : 67ºN, 18ºE), s'étend sur 12 000 km^2 et le paysage est caractérisé par des montagnes (vallées profondes, glaciers et hauts plateaux atteignant jusqu'à 2 000 m d'élévation) et collines. Le site d'étude au sud (localisation approximative : 61ºN, 15ºE) s'étend sur 13 000 km^2 et le paysage est caractérisé par des collines à faible élévation (200 - 1 000 m). La forêt est principalement composée de pin sylvestre (*Pinus sylvestris*), d'épinette de Norvège (*Picea abies*) et de bouleaux (*Betula* sp.) dans les deux sites d'études. Toutefois, la sylviculture est intensive dans le sud. Le suivi des ours brun couvre les années 1984-2011 dans le nord, et 1985-aujourd'hui dans le sud. Les deux sites d'étude présentent d'importantes différences

en termes de densité de population (plus faible au nord), conditions climatiques (plus difficiles au nord) et d'intensité d'activité humaine (plus faible au nord; Dahle *et al.*, 2006).

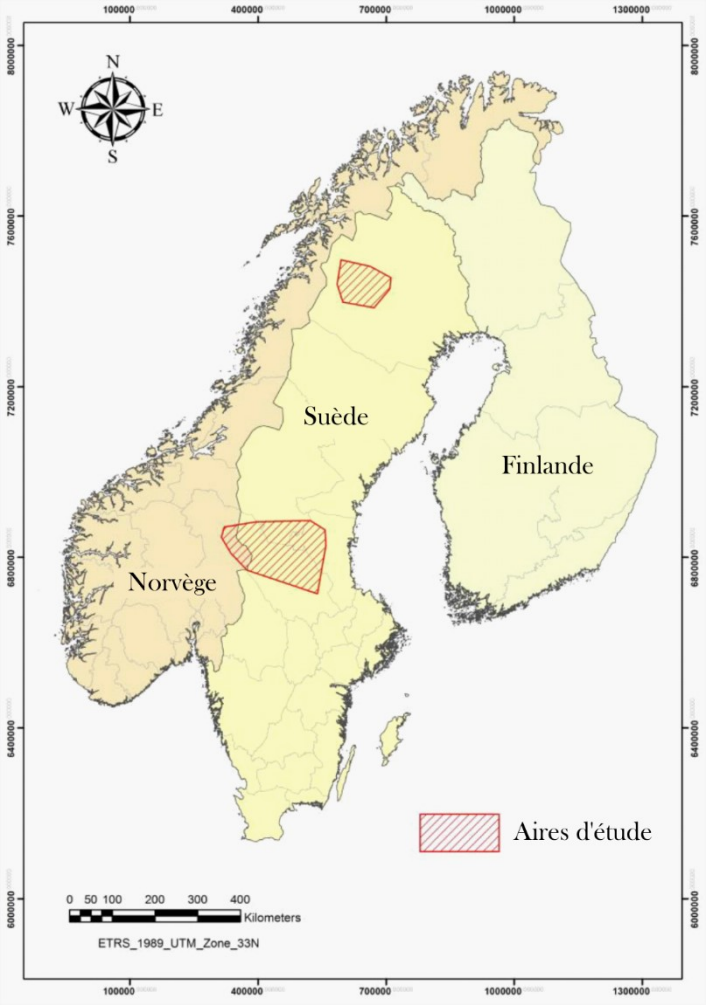

Figure 1.6 Carte présentant les deux aires d'études (régions hachurées en rouge) du SBBRP.

Carte adaptée de Esteruelas (2017).

1.9 Méthodologie générale

Dans le cadre de mon projet de doctorat, j'ai utilisé les données issues du suivi à long-terme de la population d'ours brun scandinave récoltées par le SBBRP. L'objectif premier du SBBRP est de fournir des informations sur la distribution, les mouvements, l'écologie et l'abondance de la population afin d'informer les autorités chargées de la gestion des ours bruns en Scandinavie (Swenson *et al.*, 1998). Pour ce faire, la méthode principale du SBBRP est de suivre des femelles ours brun de la naissance jusqu'à la mort, ce qui permet de récolter des informations sur les traits d'histoire de vie (âge à la première reproduction, taille de portée, durée des soins maternels, etc.), la démographie (taille de population, taux de survie, etc.) et les comportements (déplacements, sélection d'habitat, etc.). Les ours sont capturés au printemps à l'émergence de la tanière par injection d'une drogue anesthésiante (combinaison de Tiletamine, Zolazepam et hypochlorides de Médétomidine) projectée par un fusil à fléchette à partir d'un hélicoptère (Arnemo *et al.*, 2011). À la capture (Figure 1.7), plusieurs mesures sont prises (p. ex. masse) et des échantillons sont prélevés (p. ex. tissus pour analyses génétiques). Les ours sont équipés de colliers VHF (1985-2003) et d'une combinaison de VHF et GPS-GSM (2003-aujourd'hui dans le sud), ce qui permet les relocalisations et l'extraction d'informations spatiales (p. ex. utilisation de l'espace). Pour des considérations éthiques, les oursons de l'année ne sont pas capturés; seuls les groupes familiaux comprenant des oursons d'un an le sont. Le suivi d'individus concerne majoritairement les femelles, mais des captures de mâles sont aussi réalisées, mais de façon plus opportuniste.

Figure 1.7 **Femelle ours brun anesthésiée chimiquement par le SBBRP pour l'identification et la collecte de mesures (p. ex. masse, taille).**
Crédit photo : Joanie Van de Walle.

CHAPITRE 2
COMPROMIS ENTRE TAILLE ET NOMBRE DE JEUNES

2.1 Description de l'article et contribution

L'idée de cet article est venue d'un constat simple : il existe une grande diversité phénotypique entre les jeunes d'une même mère. Bien que ce constant semble évident, il est étonnamment très peu considéré dans la littérature scientifique. En effet, on commence seulement à s'intéresser à comprendre les mécanismes générant cette diversité et plusieurs hypothèses sont avancées, mais très peu sont encore testées en milieu naturel, et encore moins sont validées. Dans cet article, nous ne tentons pas d'expliquer le phénomène, mais partons plutôt de ce constat de base pour vérifier l'hypothèse selon laquelle il existerait une hétérogénéité dans le compromis entre la masse et le nombre de jeunes au sein des portées. L'objectif était donc de vérifier si 1) la masse des jeunes diminue au sein des plus grandes portées et si 2) la masse des plus petits oursons décline avec la taille de la portée. Nous montrons que seule la masse des plus petits oursons décline avec la taille de portée (la masse des plus gros oursons, elle, demeure inchangée), ce qui suggère que les coûts énergétiques liées à de plus grandes portées sont portés exclusivement par une petite partie de la portée : les plus petits oursons.

Je suis à l'origine de l'idée pour cet article. J'ai réalisé les analyses statistiques avec les suggestions de Fanie Pelletier. J'ai écrit la première version du manuscrit. Fanie Pelletier, Andreas Zedrosser et Jon E. Swenson ont contribué via leurs commentaires et suggestions à l'interprétation des résultats et l'écriture des versions subséquentes de l'article. Jon E. Swenson et Andreas Zedrosser ont coordonné les activités du SBBRP et m'ont permis l'accès aux données. DOI : 10.1098/rsbl.2019.0707.

Trade-off between offspring mass and number: the lightest offspring bear the costs

Biology Letters (2020) 16 : 20190707

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https://doi.org/10.1098/rsbl.2019.0707

2.2 Abstract

Life history theory predicts a trade-off between offspring size and number. However, the role of intra-litter phenotypic variation in shaping this trade-off is often disregarded. We compared the strength of the relationship between litter size and mass from the perspective of the lightest and the heaviest yearling offspring in 110 brown bear litters in Sweden. We showed that the mass of the lightest yearlings decreased with increasing litter size, but that the mass of the heaviest yearling remained stable, regardless of litter size. Consistent with a conservative reproductive strategy, our results suggest that mothers maintained a stable investment in a fraction of the litter, while transferring the costs of larger litter size to the remaining offspring. Ignoring intra-litter phenotypic variation may obscure our ability to detect a trade-off between offspring size and number.

Keywords: Life history trade-offs, individual heterogeneity, litter size, offspring mass

2.3 Introduction

Under limited resources, parents must make decisions regarding energy allocation to reproduction, implying reduced allocation to other functions [1,2]. Species producing multiple offspring simultaneously face an additional dilemma; invest in either a few large or several small, offspring [3]. Evidence of the trade-off between offspring size and number at the interspecific level abounds [2,4]. Opposing results are found at the intraspecific level [5], but accounting for the masking effects of environmental conditions and individual heterogeneity [6] has helped clarify this trade-off in several species [7,8].

Many studies investigating trade-offs between offspring mass and number consider the average effect of litter/clutch size [9–13] assuming that, in a given environment, parents should produce an optimal number of offspring [9] and allocate resources equally among them [3]. This assumption is challenged however by empirical observations showing large within litter/clutch variation in offspring mass [14]. Reasons for such variation are still poorly understood, but several explanations have been proposed. For example, mothers may be unable to provision their offspring equally, especially younger mothers in adverse environmental conditions [15]. Further, offspring can actively influence how much energy is directed towards them, through differential solicitation and sibling competition, causing variation in sibling mass [16,17].

Maternal effects and strategies can also generate phenotypic variation among offspring. Diversified bet-hedging (i.e., diversification of offspring phenotypes [18]) may be a female strategy to minimise between-year variation in reproductive success under unpredictable environmental conditions [14,18], although its adaptive significance and occurrence in nature remain unclear [15,19]. In egg-producing species, asynchronous hatching can create intra-clutch phenotypic variation [20], and mothers can adjust investment differentially

following egg order [21]. In many bird species, mothers produce a caste of larger ("core") and a caste of smaller ("marginal"), expendable nestlings within the same clutch [22]. Whether adaptive or not, large within-litter/clutch individual phenotypic heterogeneity suggests that the trade-off between offspring mass and number may be borne differently by offspring from the same mother.

We investigated the trade-off between offspring mass and number in brown bears (*Ursus arctos*) and compared its importance for the lightest and the heaviest yearlings in a litter. Brown bear mothers give birth to 1-4 cubs during hibernation. Cubs separate from their mother after den emergence in their second or third spring in Scandinavia [23]. Although knowledge of the relative and temporal contribution of milk in cubs' diet is limited, cubs start feeding on solid food in their first summer, but continue to nurse throughout summer and fall [24], probably also after entering the den. Thus, maternal milk may represent the most important food source for cubs in their first year. Previous studies have shown that yearling mass decreases with litter size [12,25] and is more variable in larger litters [25], suggesting heterogeneity in the response of individual yearling mass to litter size. By adding 8 years of recently collected data, we expected to confirm the negative relationship between yearling mass and number. Then, we predicted a stronger negative relationship between yearling mass and litter size when investigated from the perspective of the lightest compared to the heaviest yearling, suggesting that smaller yearlings bear the energetic cost of the trade-off between offspring mass and number.

2.4 Methods

We used data on brown bear family groups collected during captures from a helicopter by darting conducted in late April-early May in south-central Sweden, 1990-2016. For further details on bear captures see Arnemo et al. (2011) [26]. Females were equipped with VHF

(before 2003) or VHF/GPS (after 2003) collars. For ethical reasons, only family groups with yearlings (~15 months old), not cubs-of-the-year (hereafter "cubs"), were captured. Upon capture, we determined yearling sex, and weighed all bears with a spring scale. As a surrogate for maternal size, head circumference (cm), reflecting skeletal size [10,25], was measured at the widest part of the zygomatic arch between eyes and ears with a tape. Because bears were usually captured within 2 weeks [25], yearling mass was not adjusted for capture date. Age of mothers followed since birth (54%) was known; a premolar tooth was extracted for age determination [27] for others. Although not captured, mothers with cubs were located and cubs counted from the ground or a helicopter at least three times annually. Because yearling mass can increase after partial litter loss [12], we only considered litters with no pre-capture loss (73% of litters).

Population density commonly affects body mass in large mammals [28], such as the brown bear [25]. Thus, we calculated a relative index of local population density for each family group during the yearling year by extracting a weighted mean of local density within a circular buffer of 7.16 km (average home range radius for an adult female with yearlings [29]) around the median of bear locations using VHF data prior to 2003 and a combination of VHF and GPS data from 2003 onward. Annual maps of bear density were constructed using scat-derived DNA collections conducted at the county level in specific years [30], corrected for annual trends using country-wide sightings of bears in the fall through the Swedish Large Carnivore Observation Index [31]. See Appendix 2.1 for more details on density estimation.

First, we tested for the presence of a trade-off between offspring mass and number ("average effect") using linear mixed effect models, with yearling body mass (log-transformed to meet model assumption of homoscedasticity [32]) as response variable. Litter size (set as continuous [25]) and other variables known or expected to affect yearling mass, i.e., maternal size, offspring sex, litter sex ratio, and population density index

[12,25], were included as fixed effects. To account for the potential masking effect of female size on life-history trade-offs [6,33], we included an interaction between maternal size and litter size. Random effects included year of capture and litter identity nested in maternal identity.

Second, we compared the importance of the trade-off, i.e., the slope of the relationship, between yearling mass and number for only the lightest and heaviest yearlings within each litter ("rank effect"). To provide a baseline for statistical comparison with larger litters, singletons were also included and randomly attributed a rank ("lightest" or "heaviest"). See Appendix 2.2 for more details on yearling classification procedure. We used linear mixed effects models with log-transformed yearling mass of only the lightest and heaviest yearlings for each litter as the response variable and the same fixed and random effects structure as above, but we added an interaction term between litter size and yearling rank (2 levels: "lightest", "heaviest"). For both analyses ("average effect" and "rank effect"), the starting models included all fixed effects and we obtained the final models by backwards selection using Likelihood ratio tests. Variance Inflation Factors were all < 3. Effect sizes are presented as means of percent mass change per additional yearling in a litter with 95% confidence intervals calculated as exponentiated model coefficients subtracted by 1. All analyses were performed using R v 3.4.3 [34].

2.5 Results

We obtained data from 110 litters without litter reduction from 54 mothers (maximum 5 litters/mother), totalling 250 yearlings (122 females, 128 males) [35]. Litter size varied from 1 to 4 (1: n=14, 2: n=54, 3: n=40, 4: n=2). Due to few litters of 4, we combined litter sizes 3 and 4. There was no interactive effect of litter size and maternal size on yearling mass (Table 2.1a). Yearling mass was unaffected by maternal age and litter sex ratio, but

yearlings were heavier if they were males, their mother was larger and population density was lower. There was a significant negative relationship between yearling mass and litter size, revealing a trade-off between offspring mass and number in the population (Figure 2.1a); yearling mass decreased by 6.1% (95% CI=[-11.0%, -0.8%]) per additional yearling in a litter.

We ranked 206 yearlings as "lightest" or "heaviest". In litters of 3-4, yearlings with intermediate mass (n=44) were removed from further analyses. Within a given litter, the lightest yearlings were more often females (61%) and the heaviest were more often males (66%). Observed sex-, litter size-, and rank-specific yearling masses are presented in Appendix 2.3. We found no interactive effect of litter size and maternal size on the mass of the lightest and heaviest yearlings (Table 2.1b). The mass of lightest and heaviest yearlings was affected by maternal size and population density, but not by sex, litter sex ratio, or maternal age. However, the slope of the relationship between yearling size and litter size differed by yearling rank, i.e., there was a significant interaction between offspring rank and litter size. The lightest yearlings were affected by litter size, as mass of the lightest yearling decreased by 12.2% (95% CI=[-21.1%, -2.3%]) per additional yearling in a litter (Figure 2.1b). However, mass of the heaviest yearling was unaffected (percent mass change: 1.0%, 95% CI=[-4.6, 7.0]) by litter size (Figure 2.1b).

Table 2.1 **Final models obtained by backward selection to test for the presence of a trade-off between offspring mass and number (*a* – average effect) and whether the trade-off was borne differently by the "lightest" and "heaviest" yearlings in a litter (*b*; rank effect) in brown bears in Sweden, 1990-2016.**

				95% CI				
Variables	β	SE	t-value	Lower	Upper		Variance	SD
(a) log(Yearling mass) – Average effect *(conditional R^2 = 77%, marginal R^2 = 24%)**								
Fixed effects						Random effects		
						Litter ID ×		
Intercept	0.87	0.38	2.32	0.14	1.61	Maternal ID	0.01	0.11
Sex (male)	0.06	0.02	2.58	0.01	0.10	Maternal ID	0.01	0.08
Litter size	-0.06	0.03	-2.28	-0.12	-0.01	Year	0.03	0.17
Maternal size	0.04	0.01	6.36	0.03	0.05	Residual	0.02	0.14
Local density	-0.26	0.10	-2.57	-0.47	-0.06			
Variables excluded: Litter size × Maternal size (χ^2=0.08, P=0.78), Maternal age (χ^2=0.98, P=0.32), Sex ratio (χ^2=2.52, P=0.11)								
(b) log(Yearling mass) – Rank effect *(conditional R^2 = 91%, marginal R^2 = 33%)*								
Fixed effects						Random effects		
						Litter ID ×		
Intercept	0.77	0.37	2.05	0.04	1.49	Maternal ID	0.02	0.13
Litter size	0.01	0.03	0.35	-0.05	0.07	Maternal ID	0.01	0.07
Maternal size	0.04	0.01	6.65	0.03	0.05	Year	0.03	0.18
Local density	-0.23	0.10	-2.35	-0.43	-0.04	Residual	0.01	0.09
Rank (lightest)	0.15	0.06	2.44	0.03	0.28			
Litter size × Rank	-0.14	0.03	-5.56	-0.19	-0.09			
Variables excluded: Litter size × Maternal size (χ^2=0.06, P = 0.81), Sex (χ^2=0.00, P = 0.99), Sex ratio (χ^2 =0.00, P = 0.96), Maternal age (χ^2 = 0.85, P = 0.36)								

*Marginal and conditional R^2 refer to variance explained by fixed effects alone and both fixed and random effects, respectively [36].

2.6 Discussion

Based on life-history theory, offspring mass should decline as the number of offspring increases [2]. However, large intra-litter variation in offspring mass suggests heterogeneity in the response of individual offspring to increasing litter size. Our objective was to contrast the strength of the trade-off among offspring from the same litter. We found a non-homogenous trade-off between yearling mass and number. Indeed, the mass of the lightest yearling in a litter declined with litter size, whereas the mass of the heaviest yearling remained stable, regardless of litter size. Similar results were found using only litter sizes of 2 and 3-4 (Appendix 2.4), thus reinforcing our conclusion. Our results suggest that smaller offspring bear the cost of the trade-off between offspring mass and number in brown bears.

The heaviest yearlings in litters ≥2 were as heavy as singletons, suggesting that mothers allocate resource disproportionately among offspring regardless of litter size, raising at least one heavy yearling. In birds, parents often "play favourite", preferentially directing energy towards some nestlings and only "surplus" energy (if any) to others [22]. In ungulates producing singletons, mothers usually follow a conservative tactic, transferring the cost of current reproduction to subsequent offspring [33,37] through reduced mass gain and survival [33]. Further, despite the absence of an absolute sex-related mass difference between heaviest and lightest yearlings, heaviest yearlings within a given litter were mostly males. Sons often receive biased maternal allocation, compared to daughters, in polygynous species exhibiting sexual dimorphism [38] to improve their future reproductive success [39]. Biased allocation towards males can increase the energetic costs of reproduction when producing male offspring [40–42], which might be transferred to litter mates, as reflected by the lower mass of the lightest yearlings within a litter, especially in larger litters.

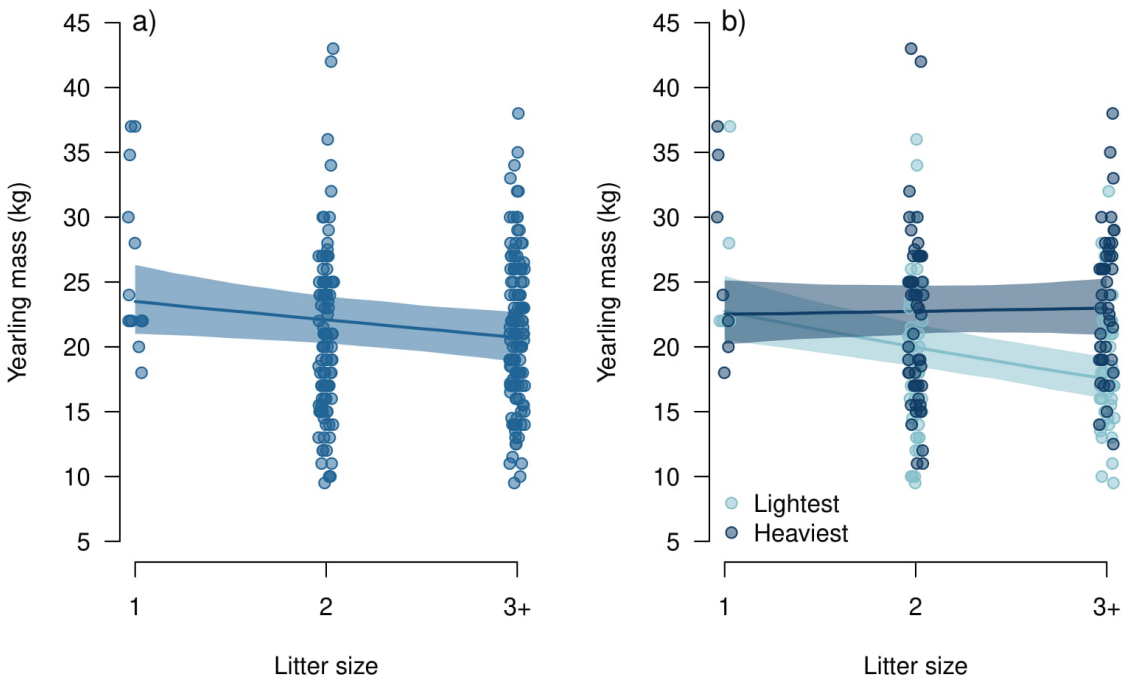

Figure 2.1 **Trade-off between offspring mass and number in brown bears from Sweden, 1990-2016, investigated using (*a*) all and (*b*) only the lightest (light blue) and heaviest (dark blue) yearlings from a litter.**

Represented are observations (circles) with model predictions (lines) and 95% confidence intervals (polygons) back-transformed to the original scale for males (a) or both sexes (b) from average-sized mothers (a,b) and at average population density (a,b).

Brown bear cubs nurse throughout their first year [24], suggesting that differential maternal provisioning should persist to yearling age. Our study includes yearlings consuming solid food, however its relative contribution to the diet is unknown. Access to food resources (mainly berries in autumn [43]), and thus foraging opportunities, should be similar among litter mates, although scramble competition or compensatory feeding is possible [44]. Evaluating the persistence of the trade-off over developmental stages and relative

contribution of maternal provisioning would help determine the role of maternal effects in brown bears, although ethical considerations made this impossible here. The persistence of the trade-off between offspring mass and number may vary among species with different feeding strategies and parental control over food access.

Life-history trade-offs can be masked by environmental conditions and individual differences in energy allocation [6], and costs of reproduction are difficult to detect empirically [45]. We show the potential for between-offspring individual variation to obscure the trade-off between offspring mass and number. Focusing on mean offspring mass may hinder our ability to detect, or cause an underestimation of, the cost of producing larger litters, which may be borne by only a fraction of the offspring. This could explain, in part, why a large number of empirical studies have failed to detect this trade-off [46]. Mass at independence can affect an individual's future survival and reproductive success [47,48] (but see [49]). Being born into a large litter may thus have long-term fitness consequences for offspring, depending on their relative size, especially for female brown bears, as lifetime reproductive success is determined by their mass as yearlings [50]. From a mother's perspective, however, favouring one offspring in a large litter may result in a stable fitness return that can be augmented under conditions favouring the fitness of "extra" offspring.

2.7 Ethics

Handling of study animals was approved by the Swedish Board of Agriculture (no. 35-846/03, no. 31-7885/07, no. 31 11102/12), Uppsala Ethical Committee on Animal Experiments (no. C40/3, no. C47/9, no. C7/12) and Swedish Environmental Protection Agency (no. 412-7327-09Nv).

2.8 Data accessibility

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.b2rbnzs99 [35].

2.9 Authors' contributions

J.V.d.W. and F.P. conceived and designed the study. A.Z. and J.E.S. coordinated the project and data collection. J.V.d.W. analysed the data and wrote the first draft. All authors contributed to the interpretation of the data and subsequent manuscript writing and revisions. All authors agreed to be held accountable for the content therein and approve the final version.

2.10 Competing interests

We declare we have no competing interests

2.11 Funding

J.V.d.W. and F.P. were funded by the Natural Sciences and Engineering Research Council of Canada (PGSD2-504356-2017, CRSNG-355492, CRC-229221). The Scandinavian Brown Bear Research Project is funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, and the Austrian Science Fund.

2.12 Acknowledgments

We are grateful to everyone who have contributed to the data collection. We also thank the Quebec Centre for Biodiversity Science. This is SBBRP scientific paper number 289. This research is published as part of the NFR project 269863 BearConnect.

2.13 References

1. Stearns SC. 1992 *The evolution of life histories*. Oxford: Oxford University Press.

2. Stearns SC. 1989 Trade-offs in life-history evolution. *Funct. Ecol.* **3**, 259–268. (doi:10.2307/2389364)

3. Smith CC, Fretwell SD. 1974 The optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506. (doi:10.1086/282929)

4. Charnov EL, Ernest SKM. 2006 The offspring-size/clutch-size trade-off in mammals. *Am. Nat.* **167**, 578–582. (doi:10.1086/501141)

5. Bernardo J. 1996 The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.* **36**, 216–236. (doi:10.1093/icb/36.2.216)

6. van Noordwijk AJ, de Jong G. 1986 Acquisition and allocation of resources: their influence on variation in life history tactics. *Am. Nat.* **128**, 137–142. (doi:10.1086/284547)

7. Dziminski MA, Vercoe PE, Roberts JD. 2009 Variable offspring provisioning and fitness: a direct test in the field. *Funct. Ecol.* **23**, 164–171. (doi:10.1111/j.1365-2435.2008.01480.x)

8. Smiseth PT, Andrews CP, Mattey SN, Mooney R. 2014 Phenotypic variation in resource acquisition influences trade-off between number and mass of offspring in a burying beetle. *J. Zool.* **293**, 80–83. (doi:10.1111/jzo.12115)

9. Mappes T, Koskela E, Ylönen H. 1995 Reproductive costs and litter size in the bank vole. *Proc. R. Soc. B Biol. Sci.* **261**, 19–24. (doi:10.1098/rspb.1995.0111)

10. Derocher AE, Stirling I. 1998 Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). *J. Zool. London* **245**, 253–260. (doi:10.1017/S095283699800702X)

11. Humphries MM, Boutin S. 2000 The determinants of optimal litter size in free-ranging red squirrels. *Ecology* **81**, 2867–2877. (doi:10.1890/0012-9658(2000)081[2867:TDOOLS]2.0.CO;2)

12. Gonzalez O, Zedrosser A, Pelletier F, Swenson JE, Festa-Bianchet M. 2012 Litter reductions reveal a trade-off between offspring size and number in brown bears. *Behav. Ecol. Sociobiol.* **66**, 1025–1032. (doi:10.1007/s00265-012-1350-3)

13. Richardson J, Smiseth PT. 2019 Effects of variation in resource acquisition during different stages of the life cycle on life-history traits and trade-offs in a burying beetle. *J. Evol. Biol.* **32**, 19–30. (doi:10.1111/jeb.13388)

14. Marshall DJ, Bonduriansky R, Bussière LF. 2008 Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. *Ecology* **89**, 2506–2517.

15. Gossieaux P et al. 2019 Offspring mass variation in tree swallows: a case of bet-hedging ? *Ecosphere* **10**, e02607. (doi:10.1002/ecs2.2607)

16. Forbes S, Wiebe M. 2010 Egg size and asymmetric sibling rivalry in red-winged blackbirds. *Oecologia* **163**, 361–372. (doi:10.1007/s00442-010-1629-x)

17. Kamel SJ, Williams PD. 2017 Resource exploitation and relatedness: implications for offspring size variation within broods. *Oikos* **126**, 1219–1226. (doi:10.1111/oik.04034)

18. Philippi T, Seger J. 1989 Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **4**, 41–44. (doi:10.1016/0169-5347(89)90138-9)

19. Einum S, Fleming IA. 2004 Environmental unpredictability and offspring size: conservative versus diversified bet-hedging. *Evol. Ecol. Res.* **6**, 443–455.

20. Bitton P-P, Dawson RD, O'Brien EL. 2006 Influence of intraclutch egg-mass variation and hatching asynchrony on relative offspring performance within broods of an altricial bird. *Can. J. Zool.* **84**, 1721–1726. (doi:10.1139/z06-179)

21. Laaksonen T. 2004 Hatching asynchrony as a bet-hedging strategy - an offspring diversity hypothesis. *Oikos* **104**, 616–620. (doi:10.1111/j.0030-1299.2004.12858.x)

22. Forbes S, Thornton S, Glassey B, Forbes M, Buckley NJ. 1997 Why parent birds play favourites. *Nature* **390**, 351–352. (doi:10.1038/37025)

23. Steyaert SMJG, Endrestøl A, Hackländer K, Swenson JE, Zedrosser A. 2012 The mating system of the brown bear Ursus arctos. *Mamm. Rev.* **42**, 12–34. (doi:10.1111/j.1365-2907.2011.00184.x)

24. Farley SD, Robbins CT. 1995 Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Can. J. Zool.* **73**, 2216–2222. (doi:10.1139/z95-262)

25. Dahle B, Zedrosser A, Swenson JE. 2006 Correlates with body size and mass in yearling brown bears (*Ursus arctos*). *J. Zool.* **269**, 273–283. (doi:10.1111/j.1469-7998.2006.00127.x)

26. Arnemo JM, Evans A, Fahlman Å. 2011 *Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx.* Evenstad, Norway: Hedmark University College.

27. Matson G, Van Daele L, Goodwin E, Aumiller L, Reynolds H, Hristienko H. 1993 *A laboratory manual for cementum age determination of Alaska bear first premolar teeth*. Milltown: Matson's Laboratory.

28. Fowler CW. 1987 A review of density dependence in populations of large mammals. In *Current mammalogy* (ed HH Genoways), New-York: Plenum Press.

29. Dahle B, Swenson JE. 2003 Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *J. Anim. Ecol.* **72**, 660–667. (doi:10.1046/j.1365-2656.2003.00737.x)

30. Bellemain E, Swenson JE, Tallmon D, Brunberg S, Taberlet P. 2005 Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. *Conserv. Biol.* **19**, 150–161. (doi:10.1111/j.1523-1739.2005.00549.x)

31. Kindberg J, Swenson JE, Ericsson G, Bellemain E, Miquel C, Taberlet P. 2011 Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biol.* **17**, 114–123. (doi:10.2981/10-100)

32. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. New York: Springer.

33. Festa-Bianchet M, Côté SD, Hamel S, Pelletier F. 2019 Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction. *J. Anim. Ecol.* **88**, 1118–1133. (doi:10.1111/1365-2656.13002)

34. R Core Team. 2016 *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing

35. Van de Walle J, Zedrosser A, Swenson J, Pelletier F. 2019 Data from: Trade-off between offspring mass and number: the lightest bear the cost. Dryad Digital Repository (doi:10.5061/dryad.b2rbnzs99)

36. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x)

37. Gaillard J-M, Yoccoz NG. 2003 Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* **84**, 3294–3306. (doi:10.1890/02-0409)

38. Landete-Castillejos T, García A, López-Serrano FR, Gallego L. 2005 Maternal quality and differences in milk production and composition for male and female Iberian red deer calves (*Cervus elaphus hispanicus*). *Behav. Ecol. Sociobiol.* **57**, 267–274. (doi:10.1007/s00265-004-0848-8)

39. Trivers RL, Willard DE. 1973 Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**, 90–92. (doi:10.1126/science.179.4068.90)

40. Lee PC, Moss CJ. 1986 Early maternal investment in male and female African elephant calves. Behav. *Ecol. Sociobiol.* **18**, 353–361. (doi:10.1007/BF00299666)

41. Gomendio M, Clutton-Brock TH, Albon SD, Guinness FE, Simpson MJ. 1990 Mammalian sex ratios and variation in costs of rearing sons and daughters. *Nature* **343**, 261–263. (doi:10.1038/343261a0)

42. Douhard M, Festa-Bianchet M, Pelletier F. 2016 Maternal condition and previous reproduction interact to affect offspring sex in a wild mammal. *Biol. Lett.* **12**, 20160510. (doi:10.1098/rsbl.2016.0510)

43. Stenset NE et al. 2016 Seasonal and annual variation in the diet of brown bears Ursus arctos in the boreal forest of southcentral Sweden. *Wildlife Biol.* **22**, 107–116. (doi:10.2981/wlb.00194)

44. Sikes RS. 1998 Tradeoffs between quality of offspring and litter size: differences do not persist into adulthood. *J. Mammal.* **79**, 1143–1151. (doi:10.2307/1383005)

45. Reznick D. 1985 Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**, 257–267. (doi:10.2307/3544698)

46. Christians JK. 2002 Avian egg size: variation within species and inflexibility within individuals. *Biol. Rev. Camb. Philos. Soc.* **77**, 1–26. (doi:10.1017/S1464793101005784)

47. Fedak MA, Anderson SS. 1982 The energetics of lactation: accurate measurements from a large wild mammal, the Grey seal (*Halichoerus grypus*). *J. Zool.* **198**, 473–479. (doi:10.1111/jzo.1982.198.4.473)

48. Beauplet G, Barbraud C, Chambellant M, Guinet C. 2005 Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate and oceanographic conditions. *J. Anim. Ecol.* **74**, 1160–1172. (doi:10.1111/j.1365-2656.2005.01016.x)

49. Oksanen TA, Jonsson P, Koskela E, Mappes T. 2001 Optimal allocation of reproductive effort : manipulation of offspring number and size in the bank vole. *Proc. R. Soc. London B* **268**, 661–666. (doi:10.1098/rspb.2000.1409)

50. Zedrosser A, Pelletier F, Bischof R, Festa-Bianchet M, Swenson JE. 2013 Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations. *Ecology* **94**, 231–240. (doi:10.1890/12-0229.1)

CHAPITRE 3

DÉTERMINANTS DIRECTS ET INDIRECTS DE LA DURÉE DES SOINS MATERNELS

3.1 Description de l'article et contribution

On en connaît très peu sur les causes de variation dans la durée des soins maternels, bien qu'il s'agisse d'un trait d'histoire de vie d'intérêt en écologie des populations. Cet article visait donc à évaluer la contribution directe et indirecte des caractéristiques maternelles et liées à la portée ayant le potentiel d'influencer la durée des soins maternels chez l'ours brun scandinave. Dans cet article, j'ai utilisé une méthode statistique robuste, c.-à-d. les analyses de piste, ce qui m'a permis d'identifier et de départager les contributions des déterminants de la durée des soins maternels. Pour cet article, j'ai utilisé les données issues des suivis à long-terme du nord et du sud de la Suède afin d'augmenter la taille d'échantillon, mais aussi pour tenir compte des différences obtenues avec une étude précédente réalisée sur la population au nord de la Suède. L'inclusion des deux populations a aussi permis de comparer les contributions relatives des déterminants de la durée des soins maternels dans des contextes environnementaux différents.

Je suis l'instigatrice de l'étude et j'ai développé l'idée originale. J'ai réalisé les analyses statistiques et écrit la première version de l'article. Fanie Pelletier, Andreas Zedrosser et Jon E. Swenson ont contribué à l'élaboration de l'idée et aux révisions de l'article. Jon E. Swenson et Andreas Zedrosser ont coordonné le SBBRP.

Disentangling direct and indirect determinants of the duration of maternal care in brown bears: environmental context matters

En révision à *Journal of Animal Ecology*

Joanie Van de Walle, Andreas Zedrosser, Jon E. Swenson et Fanie Pelletier

3.2 Abstract

1. The duration of maternal care, an important life history trait affecting population dynamics, varies greatly within species. Yet, our understanding of its predictors is limited, mostly correlative, and subject to misinterpretations due to difficulties to disentangle the role of maternal- and offspring-related characteristics.

2. We conducted path analysis on a dataset including 207 brown bear litters captured over a 29-year period in two populations in Sweden ("North" and "South") facing contrasting environmental conditions to identify and quantify the causes of variation in the duration of maternal care (1.5 years or 2.5 years).

3. We showed that the causal determinants of the duration of maternal care were context dependent. Contrary to their expected central role in the determination of the duration of maternal care, yearling mass and its direct determinants (i.e., litter size and maternal mass) were only important in the North population, where environmental conditions are harsher. In the South, the duration of maternal care was only affected by maternal age; older females provided longer maternal care. This result may be explained by the hunting regulation protecting members of family groups coupled with the high hunting pressure in this area, allowing females providing longer maternal care to survive longer.

4. Our results provide an important contribution to our very limited knowledge of the direct and indirect determinants of the duration of maternal care and highlight the importance of accounting for the environmental context when assessing maternal reproductive tactics.

Key-words: Maternal care, path analysis, brown bear, weaning age, harvest

3.3 Introduction

Parental care refers to all parental behaviours yielding short- and/or long-term benefits to offspring in terms of growth, survival, and reproduction (Clutton-Brock, 1991; Smiseth, Kölliker, & Royle, 2012). Through the improvement of offspring fitness, care can also contribute to the inclusive fitness of parents (Hamilton, 1964). However, the time and energy spent, and risk incurred, by parents while providing care (i.e., parental expenditure; Clutton-Brock 1991) can be high and reach a level where it entails fitness costs (i.e., parental investment; Trivers 1972). Natural selection should thus favour optimal levels of parental care maximising offspring fitness while limiting parental fitness costs.

When the costs of parental care outweigh their benefits, care should terminate and offspring be weaned (Davies, Krebs, & West, 2012; Trivers, 1974; Williams, 1966). In mammals, where parental care is provided almost exclusively by females (Clutton-Brock, 1991) and mostly takes the form of milk provisioning (Gittleman & Thompson, 1988), weaning is typically attained when offspring can survive on a milk-free diet (Borries, Lu, Ossi-Lupo, Larney, & Koenig, 2014). However, in species where other forms of care can also be provided after nutritional independence (e.g., protection, teaching and assistance; Clutton-Brock, 1991) and/or in species where females resume their reproductive activities only

once maternal care ceases (Borries et al., 2014), the total duration of maternal care may better reflect maternal expenditure. Indeed, in several species, the duration of maternal care is directly linked with interbirth intervals and reproductive rates and ultimately population dynamics (Van de Walle, Pigeon, Zedrosser, Swenson, & Pelletier, 2018). Thus, identifying the determinants of the duration of maternal care is important from both ecological and management perspectives.

The duration of maternal care varies greatly between and within mammals. For example, lactation ranges from only 4 days in the hooded seal, *Cystophora cristata* (Bowen, Oftedal, & Boness, 1985) to up to 8 years in the African elephant, *Loxodonta africana* (Lee & Moss, 1986). At the intra-specific level, empirical studies also report large variations in the duration of maternal care, ranging from days, months, and even years (e.g., Balme, Robinson, Pitman, & Hunter, 2017; Bowen, Ellis, Iverson, & Boness, 2001; Lee & Moss, 1986). Despite having the potential to affect long-term reproductive success and fitness of individual females (Balme et al., 2017; Van de Walle et al., 2018), our knowledge of the causal mechanisms leading to variation in the duration of maternal care is surprisingly limited.

Lee, Majluf, and Gordon (1991) showed in a metanalysis that offspring age and mass at weaning are correlated across several mammalian species, with offspring being weaned at the threshold mass of about four times their neonatal mass. Despite its inter-specific focus, these findings suggest flexibility in the duration of maternal care, depending on offspring body condition, at the intra-specific level (Lee, 1996). Early weaning should be advantageous for females in good condition, which may wean offspring in good condition quickly and resume reproduction sooner (Lee et al., 1991), thereby increasing lifetime reproductive success (Fairbanks & McGuire, 1995). In less favourable conditions, females may face challenges in acquiring sufficient resources for optimal offspring growth and the duration of maternal care can either be reduced through offspring abandonment to favour

investment in maintenance or extended to improve offspring mass and survival prospects (Balme et al., 2017; Bowen et al., 2001; Lee et al., 1991; Lee & Moss, 1986; Trillmich, 1986). Maternal and offspring conditions should thus play a central role in determining the duration of maternal care (Lee et al., 1991), however, their relative importance may change in different environmental contexts.

Empirical studies have shown that the duration of maternal care can correlate with both maternal and offspring traits, such as condition (Trillmich, 1986), maternal age and experience (Bowen et al., 2001; Lonsdorf, Stanton, Pusey, & Murray, 2019), litter size (König & Markl, 1987; Lee, 1996), and offspring sex (Lee & Moss, 1986). However, all of these traits can correlate with offspring mass, and their effect on the duration of maternal care could be indirect. For instance, females with more reproductive experience and in better body condition have more resources to allocate to offspring growth (Georges & Guinet, 2000), leading to shorter maternal care (Lee et al., 1991). Litter size is typically linked with offspring mass, due to the trade-off between offspring size and number (Charnov & Ernest, 2006), which might explain why offspring from larger litters are weaned later (König & Markl, 1987). In polygynous species, investment in male offspring is expected to be more beneficial compared to female offspring (Trivers, 1972), which could explain why those male offspring are often larger and may attain optimal weaning mass later (Trillmich, 1986). Therefore, the role of maternal and offspring characteristics may be intertwined and there is a need to disentangle their direct and indirect contributions to the duration of maternal care.

Based on data collected over 29 years from 207 brown bear (*Ursus arctos*) litters in Sweden, our general objective was to identify and quantify the determinants of the duration of maternal care. More specifically, we aimed at identifying the determinants of the duration of maternal care, quantifying their direct and indirect causal contributions, and comparing their effects between two study populations experiencing contrasting

environmental conditions. First, we investigated which maternal (i.e., maternal mass, age, and reproductive experience) and litter (i.e., yearling mass, litter size, and sex ratio) characteristics could explain variation in the duration of maternal care. We expected a correlation between the duration of maternal care and both yearling mass and litter size, with lighter yearlings from larger litters receiving longer maternal care (Dahle & Swenson, 2003a). We also expected that heavier, older and more experienced mothers would provide shorter maternal care, and that larger and male-biased litters would receive longer maternal care. Second, using path analysis, we tested and compared seven competing causal hypotheses to identify the direct and indirect determinants of the duration of maternal care. Generally, we expected a strong causal relationship between yearling mass and the duration of maternal care. Building on this, we tested six hypotheses: 1) maternal and litter characteristics have an indirect contribution through their effects on yearling mass, 2) maternal and litter characteristics affect the duration of maternal care both directly and indirectly, and 3-6) maternal characteristics indirectly affect the duration of maternal care through their direct effects on litter characteristics. We also tested the alternative hypothesis (#7) of no causal link between yearling mass and the duration of maternal care. Third, we tested the causal hypotheses in two separate Swedish populations (North and South). In the North, climate is harsher and population density lower compared to the South (Zedrosser, Dahle, & Swenson, 2006). Due to the different environmental contexts, we expected different causal structures in the two populations. Specifically, because of the harsher climatic conditions in the North that may increase the cost of extending maternal care for females, we predicted that the duration of maternal care would be more strongly influenced by offspring and maternal mass there. Legal hunting is allowed throughout Sweden; however, its pressure is higher in the South. Only members of family groups are legally protected, which improves the survival of females providing longer maternal care in the South (Van de Walle et al., 2018). We thus expected a positive effect of maternal age on the duration of maternal care in the South.

3.4 Methods

3.4.1 Study species and data collection

The brown bear is a solitary, sexually dimorphic species, with males larger than females both as yearlings and adults (Dahle, Zedrosser, & Swenson, 2006; Steyaert, Endrestøl, Hackländer, Swenson, & Zedrosser, 2012). In Scandinavia, females give birth to 1-4 cubs in January and lactate in their winter den until den emergence in mid-April (Friebe et al., 2014; Manchi & Swenson, 2005). Females provide care (mostly lactation and protection) throughout the cubs' first year (at this stage cubs are referred to as "cubs-of-the-year") and family groups hibernate together the following winter. After den emergence the second year, females either separate from their now yearlings, or continue maternal care for an additional year (cubs are now two-year-olds; Dahle & Swenson, 2003a). Total duration of maternal care thus varies from 1.5 to 2.5 years (Van de Walle et al., 2018) and is correlated with yearling mass and litter size (Dahle & Swenson, 2003a).

We used data collected in a long-term monitoring program of brown bears in two populations (600 km apart) in Sweden. The first population (North) is located in Norrbotten County, northern Sweden (~67°N, 18°E), and the second (South) in Dalarna and Gävleborg counties, south-central Sweden (~61°N, 14°E). See (Zedrosser et al., 2006) for a detailed description of the study populations. We used data from 1993-2011 (North) and 1990-2019 (South). Females were captured and chemically immobilized by darting from a helicopter in mid-April to mid-May (Arnemo, Evans, & Fahlman, 2011). Family break-up occurs in May-July (Dahle & Swenson, 2003b), thus characteristics measured at spring capture should be representative of cues used by females to base their decision regarding separation from their yearlings. At capture, bears were equipped with a VHF (prior to 2003) or a VHF/GPS (after 2003) collar, which allowed relocation for observations and recaptures.

For ethical reasons, cubs-of-the-year were not captured. Females were captured every second year and/or when with yearling cubs and were measured and weighed with a spring scale (to the nearest 0.5 kg). Once captured, individual yearlings were also weighed, and their sex was determined. For females followed since birth, age was known; for others, a vestigial premolar tooth was extracted for age determination (Matson et al., 1993). Our dataset did not comprise any females giving birth at 26 years or older, thus we do not expect reproductive senescence (onset at 27 years in brown bears; Schwartz, Miller, & Haroldson, 2003) in our study populations. Female reproductive state (solitary or with dependent cubs, regardless of their age) was determined through visual observations from a helicopter or the ground three times annually and their reproductive experience (primiparous or multiparous) was determined from monitoring history. Because captures usually occurred within 2 weeks (Dahle et al., 2006), maternal and yearling mass were not adjusted for capture date. Yearling litter size ranged from 1 to 4, but due to few litters of 4 (n=3), we pooled litter sizes of 3 and 4 for further analyses. Litters where not all yearlings were measured (n=15) were removed from analyses. Analyses were conducted on litters rather than individual yearlings, as all yearlings in a litter separate from their mother simultaneously (Dahle & Swenson, 2003b).

3.4.2 Factors influencing the duration of maternal care

We constructed generalized linear mixed effects models using R package lme4 (Bates, Mächler, Bolker, & Walker, 2015) with 'duration of maternal care' as the response variable and maternal (maternal mass, age, and reproductive experience) and litter (average yearling mass, litter size, and sex ratio) characteristics as explanatory variables. Duration of maternal care was treated as a binomial process (0=1.5 years and 1=2.5 years), representing the probability of extending the period of maternal care beyond 1.5 years. We constructed three sets of candidate models, one for both populations combined, and one for each population separately. Within those sets, we compared 12 candidate models (Table 3.1).

The first six models contained only single variables: maternal mass (continuous; in kg), maternal age (continuous; in years), maternal reproductive experience (categorical: primiparous or multiparous), yearling mass (continuous; average mass (kg) of yearlings in a litter), litter size (continuous; from 1 to 3&4), and sex ratio (continuous; proportion of males). Then, we constructed 4 additional models based on biologically relevant combinations of variables: maternal experience (maternal age, reproductive experience), litter composition (litter size, litter sex ratio), maternal characteristics (maternal mass, age, reproductive experience), and litter characteristics (yearling mass, litter size, sex ratio). Finally, we added a global model (all variables) and a null model (intercept only). Maternal identity was added as a random intercept in all models to account for pseudoreplication. We also tested whether including year of data collection as a random intercept would improve model fit with likelihood ratio tests (Burnham & Anderson, 2002) comparing the null model including maternal identity and a model including both maternal identity and year. Year was retained as a random effect only when it significantly improved model fit. All continuous variables were scaled (mean = 0, variance = 1) prior to analyses. All VIFs were <3, suggesting that collinearity was not problematic. Correlation plots for the model variables are provided as Appendix A3.1. For each model, we extracted the difference of its Akaike's Information Criterion value corrected for small sample size (AICc; Burnham & Anderson, 2002), compared to the best performing model (AICc = 0) in our model set, along with its AICc weight ($AICc_w$). For the best model, we estimated the proportion of variance explained by fixed and the combination of fixed and random effects, using marginal and conditional delta R^2 (Nakagawa, Johnson, & Schielzeth, 2017) with the R package MuMIn (Barton, 2019).

3.4.3 Path analysis

We aimed to disentangle the causal relationships between maternal and litter characteristics and the duration of maternal care using path analysis. Path analysis, a generalization of

structural equations modelling (SEM), allows the inclusion of non-linear relationships between variables, nested structures, and non-Gaussian data distributions (Shipley, 2000). SEM and path analysis are sensitive to the ratio of variables in relation to the sample size (Shipley, 2000). Therefore, we only retained variables if their associated single variable model performed better than the null model in the first step. We specified seven causal hypotheses in the form of Directed Acyclic Graphs (DAGs; Figure 3.1) and tested independence claims between variables not linked by an arrow in the DAGs using d-separation (Shipley, 2013). For each d-separation claim, we estimated the probability of absence of correlation between variables when controlling for their hypothetical causal parents (p_i; null probability), where $p > 0.05$ suggests d-separation. We assumed a Gaussian distribution for maternal mass, maternal age, and yearling mass, and Poisson and binomial distributions for litter size and the duration of maternal care, respectively. All models included maternal identity as a random factor. We combined null probabilities for each d-separation claim using Fisher's *C* statistic (Shipley, 2013), given by equation 3.1.

$$C = -2\sum_{i=1}^{c} \ln(Pi) \qquad \text{(equation 3.1)}$$

A given DAG was accepted if the Fisher's *C* statistic followed a chi-squared distribution with $2c$ degrees of freedom (c is the number of independence claims tested). For each DAG, we calculated its corresponding AICc using equation 3.2 provided in Shipley (2013):

$$AICc = C + 2K\left(\frac{n}{n-K-1}\right) \qquad \text{(equation 3.2)}$$

where *C* is the *C* statistic, *K* is the total number of maximum-likelihood estimates from all mixed effects models included in the DAG, and *n* is the sample size. We selected the accepted DAG with the lowest AICc value to estimate relationships within the DAG. Direct contributions were estimated from slope coefficients along a direct path (e.g., A → C, with A being the direct cause of C), whereas indirect contributions were estimated by multiplying all the slope coefficients from the single arrows along an indirect path (e.g., A

→ B → C, with A indirectly causing changes in C through its direct effect on B). The total contribution of a variable is the sum of its direct and indirect contributions. Finally, we included an effect of "population" nested in each explanatory variable within the parametric model explaining the duration of maternal care from the best causal structure. This allowed population-specific statistical estimation of variable contributions to the duration of maternal care. Additionally, and because a different causal structure may explain the duration of maternal care between populations, we also tested the seven hypothetical causal structures for each population separately.

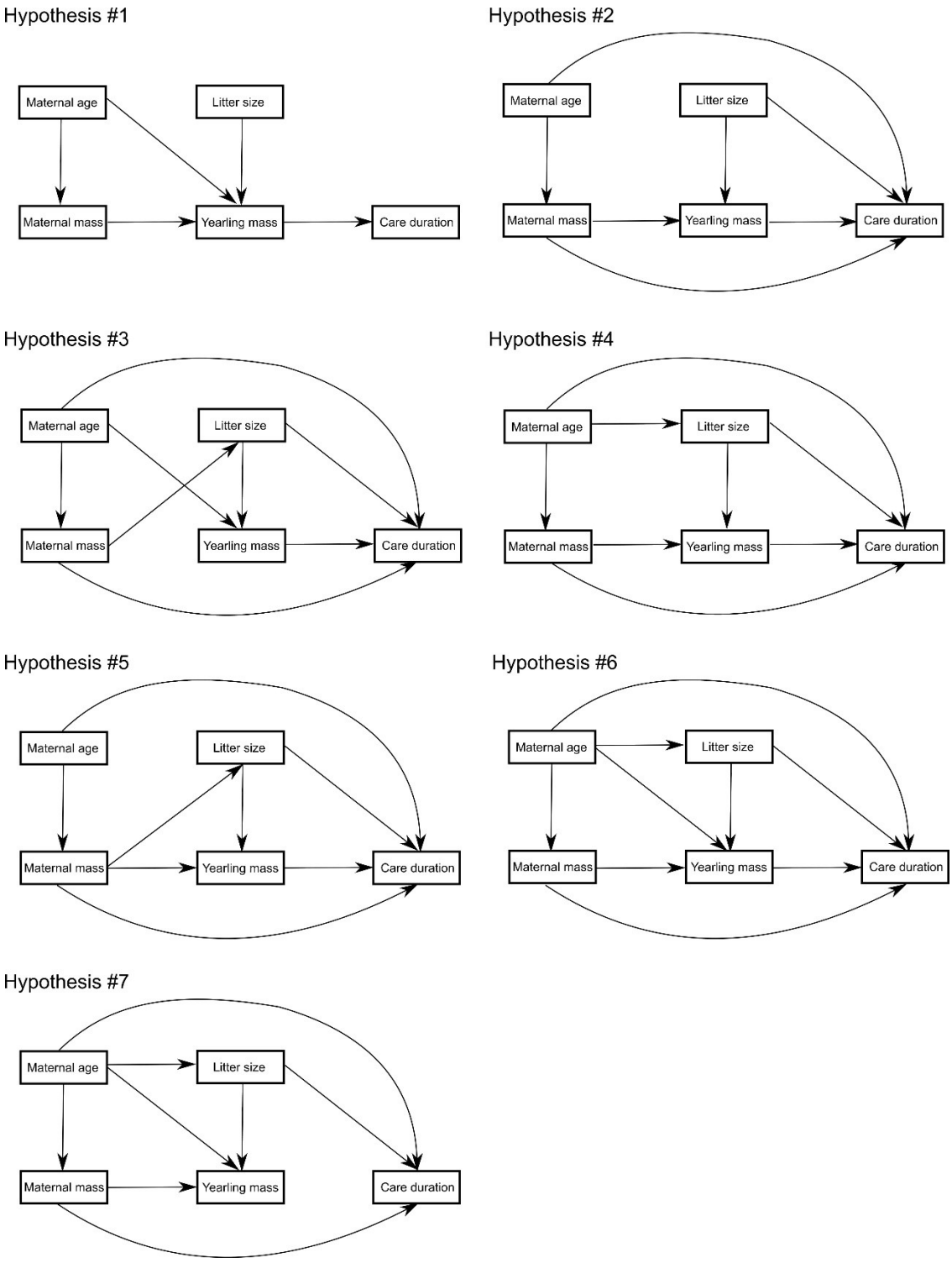

Figure 3.1 Proposed hypotheses of causal structures to explain variation in the duration of maternal care in Scandinavian brown bears, 1990-2019.

3.5 Results

3.5.1 Factors influencing the duration of maternal care

Our dataset included 207 yearling brown bear litters in both populations. For 15 litters, reproductive experience of mothers was unknown and omitting those litters resulted in a sample size of 192 litters from 92 females. Candidate model fit was not improved by including year of data collection as a random intercept (χ^2 = 2.96, P = 0.09), thus only maternal identity was retained as a random intercept. The best model explaining variation in the duration of maternal care included only litter size (Table 3.1a), i.e., the probability of continuing maternal care increased with increasing litter size (logit scale: $\beta_{\text{Litter size}}$ = 1.11, SE = 0.42, P = 0.008). Marginal and conditional delta R^2 were 0.07 and 0.51, respectively. The global model and models for litter composition and characteristics were within ΔAICc <2 of the best model. Models containing the single variables maternal mass, maternal age, litter size, and yearling mass all performed better (albeit only slightly better, except for litter size) than the null model, suggesting these variables may be important in explaining the duration of maternal care. In contrast, models including the single variables sex ratio and maternal reproductive experience did not outperform the null model.

In the North, we had complete information from 51 litters by 31 females. The model was not improved by the inclusion of year of data collection as a random intercept (χ^2 = 1.91, P = 0.17), therefore, only maternal identity was retained as random intercept in our candidate models. The best model included only yearling mass (Table 3.1b), i.e., the duration of maternal care increased with decreasing yearling mass (logit scale: $\beta_{\text{Yearling mass}}$ = -1.10, SE = 0.54, P = 0.04). Marginal and conditional delta R^2 were 0.18 and 0.37, respectively. The model including litter characteristics was within ΔAICc <2 of the best model, but only models including the single variables yearling mass and litter size outperformed the null model.

Table 3.1 **Candidate generalized mixed effects models constructed to determine variables affecting the duration of maternal care (response variable) in Scandinavian brown bears from (a) two populations (North, South) in Sweden from 1990-2019, (b) the North population from 1993-2011, and (c) the South population from 1990-2019.**

Model	K	ΔAICc	$AICc_w$
(a) Both populations			
Litter size	**3**	**0.00**	**0.29**
Maternal mass + Maternal age + Reproductive experience + Yearling mass + Litter size + Sex ratio	**8**	**0.55**	**0.22**
Litter size + Sex ratio	**4**	**0.73**	**0.20**
Yearling mass + Litter size + Sex ratio	**5**	**1.02**	**0.17**
Maternal mass + Maternal age + Reproductive experience	5	3.23	0.06
Maternal age	3	5.69	0.02
Maternal age + Reproductive experience	4	5.97	0.01
Yearling mass	3	6.09	0.01
Maternal mass	3	6.16	0.01
Null	2	7.91	0.01
Sex ratio	3	9.28	0.00
Reproductive experience	3	9.91	0.00
(b) North population			
Yearling mass	**3**	**0.00**	**0.44**
Yearling mass + Litter size + Sex ratio	**5**	**0.92**	**0.27**
Litter size	3	2.38	0.13
Litter size + Sex ratio	4	4.44	0.05
Null	2	5.16	0.03

Table 3.1 (Continued)

Maternal mass	3	6.15	0.02
Maternal age	3	6.50	0.02
Sex ratio	3	6.86	0.01
Reproductive experience	3	7.35	0.01
Maternal mass + Maternal age + Reproductive experience + Yearling mass + Litter size + Sex ratio	8	8.68	0.01
Maternal age + Reproductive experience	4	8.69	0.01
Maternal mass + Maternal age + Reproductive experience	5	9.66	0.00
(c) South population			
Litter size	**3**	**0.00**	**0.28**
Maternal age	**3**	**1.12**	**0.16**
Litter size + Sex ratio	**4**	**1.45**	**0.13**
Null	2	2.19	0.09
Maternal age + Reproductive experience	4	3.21	0.06
Maternal mass	3	3.47	0.05
Yearling mass + Litter size + Sex ratio	5	3.58	0.05
Maternal mass + Maternal age + Reproductive experience	5	3.62	0.05
Yearling mass	3	3.85	0.04
Reproductive experience	3	3.97	0.04
Sex ratio	3	4.07	0.04
Maternal mass + Maternal age + Reproductive experience + Yearling mass + Litter size + Sex ratio	8	5.14	0.02

All models included maternal identity as a random intercept. Presented in the table for each model are: the number of parameters (K), the difference in AIC value corrected for small sample with the best performing model (ΔAICc), and model weight ($AICc_w$). Models in bold are those within 2 AICc of the best performing model within each model set.

In the South, we had complete information from 141 litters by 61 females. The model was not improved by including year as a random intercept (χ^2 = 0.05, P = 0.83), so only maternal identity was kept as random intercept in our candidate models. The best performing model included only the effect of litter size (Table 3.1c), i.e., the duration of

maternal care increased marginally with increasing litter size (logit scale: $\beta_{\text{Litter size}} = 0.92$, SE = 0.50, P = 0.07). Marginal and conditional delta R^2 were 0.04 and 0.47. Models including maternal age and litter composition were within ΔAICc <2 of the best model, but only litter size and maternal age performed better than the null model.

3.5.2 Path analyses

As models including only litter sex ratio or only reproductive experience were never found to outperform the null model in the first step, these variables were omitted in the next step. We thus retained 2 maternal (maternal age, maternal mass) and 2 litter (litter size, yearling mass) characteristics in our causal hypotheses (Figure 3.1). Because our analyses excluded maternal reproductive experience, we considered the full dataset of 207 litters (North: n = 55, South: n = 152).

Only hypotheses #6 and #7 were not rejected, with hypothesis #7 having the lowest AICc value (Table 3.2a). Based on hypothesis #7, we detected a direct contribution of litter size, maternal age, and maternal mass to yearling mass (Figure 3.2; Appendix A3.2); yearlings were lighter if they were in larger litters and if their mother was older, but were larger if their mother was larger. Maternal age directly and positively affected both maternal mass and litter size. Our best model did not include a direct effect of yearling mass on the duration of maternal care. Instead, the duration of maternal care was directly (and independently of yearling mass) affected by maternal age, maternal mass, and litter size. Indeed, the probability of continuing maternal care was higher for older and lighter females and for larger litter sizes. Maternal age also indirectly contributed to the duration of maternal care along 2 additional paths (Figure 3.2): maternal age → litter size → duration of maternal care (partial effect: 0.075), and maternal age → maternal mass → duration of

maternal care (partial effect: -0.075). The total effect of maternal age on the duration of maternal care along all paths was 0.481.

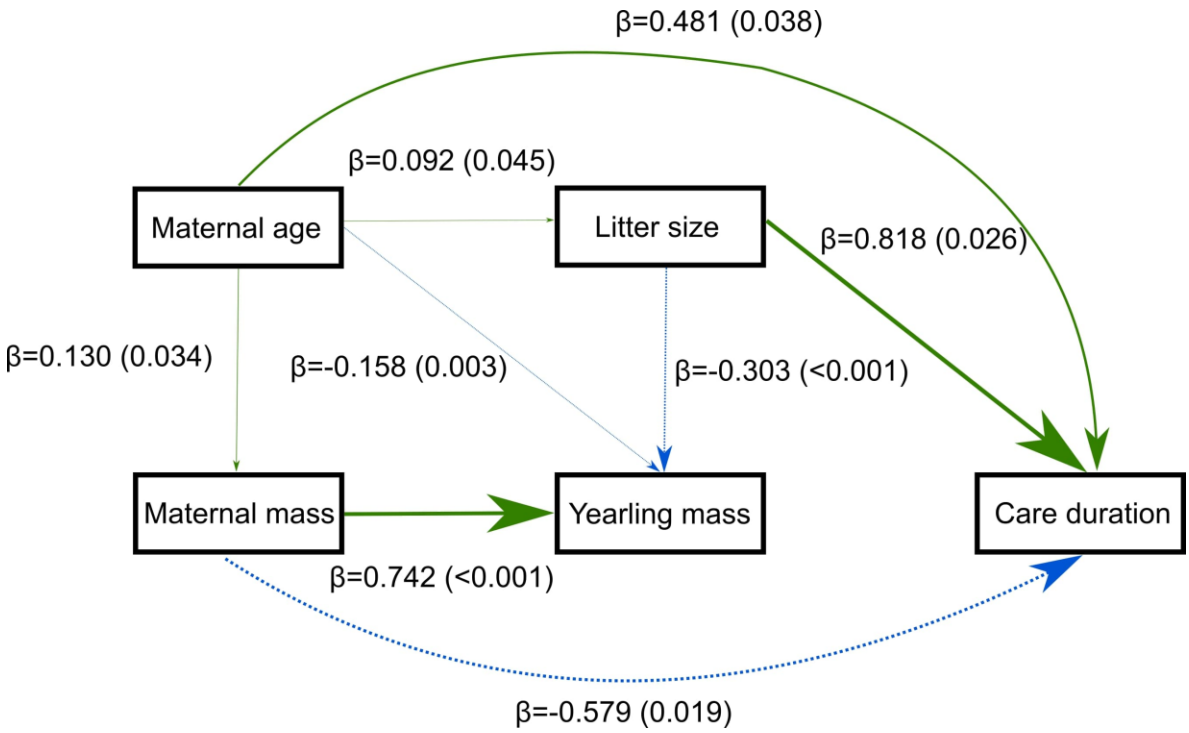

Figure 3.2 **The best of the proposed hypothetical causal structures explaining variation in the duration of maternal care in Scandinavian brown bears, 1990-2019.**

Path coefficients are presented along with their associated p-values in parenthesis. Positive relationships are represented by solid green arrows, whereas negative relationships are presented by dashed blue arrows. Arrows width is proportional to its effect size. Coefficients are presented on the transformed scaled for care duration (logit) and litter size (log).

Table 3.2 **Results from tests of d-separation claims and AICc for the seven hypotheses of causal structures (DAGs) explaining the duration of maternal care in Scandinavian brown bears from (a) two populations (North, South) in Sweden from 1990-2019, (b) the North population from 1993-2011, and (c) the South population from 1990-2019.**

Hypothesis	Fisher's *C*	df	p-value	AICc	R^2m	R^2c
(a) Both populations						
1	36.64	10	<0.001	66.83	0.04	0.36
2	31.53	6	<0.001	66.39	0.11	0.45
3	78.19	4	<0.001	122.71	0.11	0.45
4	12.87	4	0.012	57.39	0.11	0.45
5	29.18	4	<0.001	73.70	0.11	0.45
6	2.01	2	0.365	49.01	0.11	0.45
7	**2.23**	**4**	**0.694**	**46.74**	**0.11**	**0.45**
(b) North population						
1	**17.19**	**10**	**0.070**	**55.69**	**0.22**	**0.40**
2	14.00	6	0.030	60.31	0.31	0.63
3	38.64	4	<0.001	103.35	0.31	0.63
4	3.89	4	0.420	68.60	0.31	0.63
5	12.98	4	0.011	77.69	0.31	0.63
6	0.90	2	0.639	70.90	0.31	0.63
7	7.36	4	0.118	72.06	0.17	0.46
(c) South population						
1	23.81	10	0.008	54.87	0.008	0.31
2	25.36	6	<0.001	61.39	0.082	0.42
3	42.87	4	<0.001	89.28	0.082	0.42
4	14.06	4	0.007	60.47	0.082	0.42
5	23.76	4	<0.001	70.17	0.082	0.42
6	0.93	2	0.627	50.04	0.082	0.42
7	**2.62**	**4**	**0.623**	**49.04**	**0.078**	**0.42**

Marginal and conditional delta R^2 are calculated based on the parametric model explaining the duration of maternal care. The best models are in bold.

Based on the parametric model linking the duration of maternal care and its direct determinants from hypothesis #7, the importance of maternal and litter characteristics varied between populations; litter size had a significant positive effect in the North (logit scale: $\beta_{\text{Litter size}} = 1.37$, SE = 0.66, P = 0.04) but not in the South (logit scale: $\beta_{\text{Litter size}} = 0.69$, SE = 0.46, P = 0.13). In contrast, maternal age had a significant positive effect in the South (logit scale: $\beta_{\text{Maternal age}} = 0.57$, SE = 0.29, P = 0.05) but not in the North (logit scale: $\beta_{\text{Maternal age}} = 0.07$, SE = 0.44, P = 0.88). Finally, the effect of maternal mass was negative, but not significant, in the North (logit scale: $\beta_{\text{Maternal mass}} = -0.61$, SE = 0.44, P = 0.17) as well as in the South (logit scale: $\beta_{\text{Maternal mass}} = -0.43$, SE = 0.33, P = 0.18). The between-populations comparison of the importance of yearling mass on the duration of maternal care could not be tested using causal hypothesis #7, as it did not include the effect of yearling mass.

The best causal structure differed between populations. In the North, the best causal structure was hypothesis #1 (Table 3.2b). We detected a strong negative effect of yearling mass on the duration of maternal care, a strong positive effect of maternal mass on yearling mass, and a marginal effect of litter size on yearling mass (Figure 3.3; Appendix A3.2). Thus, maternal mass also had an indirect contribution ($\beta = -0.80$) to the duration of maternal care through its direct effect on yearling mass. In the South, the best causal structure was hypothesis #7 (Table 3.2c), with no effect of yearling mass on the duration of maternal care. Yearlings were lighter if their mother was older and heavier and if they were in smaller litters. The duration of maternal care was longer if females were older, and maternal mass was higher for older females. No other maternal or litter characteristics contributed directly or indirectly to the duration of maternal care in the South (Figure 3.3; Appendix A3.2).

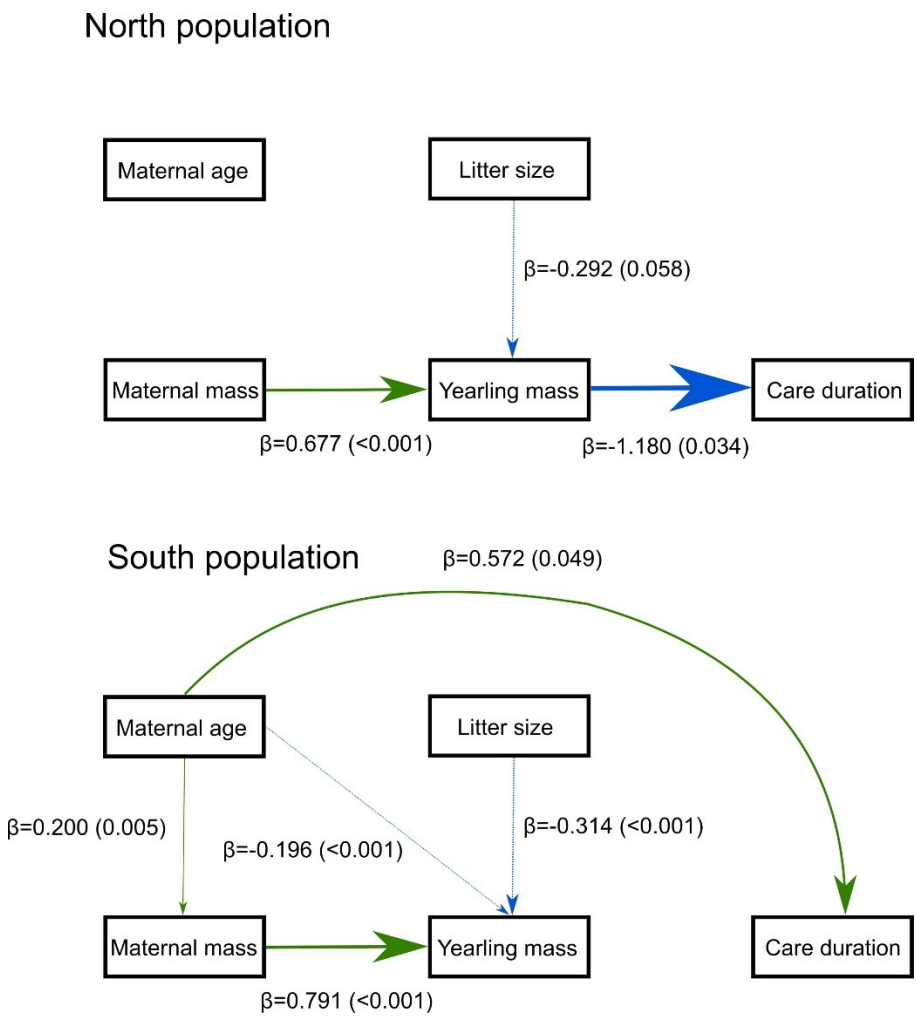

Figure 3.3 **The best of the proposed hypothetical causal structures explaining variation in the length of maternal care in Scandinavian brown bears from two study populations, North (1993-2011), and South (1990-2019).** Path coefficients are presented along with their associated p-values in parenthesis. Only significant relationships are shown. Positive relationships are represented by solid green arrows, whereas negative relationships are presented by dashed blue arrows. Arrows width is proportional to effect size. Coefficients are presented on the transformed scaled for care duration (logit) and litter size (log).

3.6 Discussion

Our objective was to identify the direct and indirect determinants of the duration of maternal care, using the Scandinavian brown bear as a model species. We found that, for brown bears throughout Sweden, the duration of maternal care was directly caused by litter size, maternal mass, and maternal age, but not by yearling mass. However, we found different causal determinants in the North and South populations, suggesting that environmental context plays an important role in shaping maternal care tactics.

Yearling mass should be a central determinant of the duration of maternal care in mammals (Lee et al., 1991). Yet, for both populations combined, yearling mass had no effect on the duration of maternal care. Instead, litter size, maternal mass, and maternal age had direct effects, independently of yearling mass. Decisions about parental effort should be driven by the optimal balance between their associated costs and benefits (Williams, 1966). Because the reproductive value of a litter increases with increasing litter size, the fitness returns of a greater parental effort when raising larger litters may outweigh the cost of reduced future reproductive success (Winkler, 1987). Parent-offspring conflicts (Trivers, 1974) are also expected to be more pronounced in larger litters (Morris, 1986), which may force females into continued maternal investment. Moreover, maternal mass directly and negatively affected the duration of maternal care, potentially because females in better body condition may be able to wean their cubs earlier (Bowen et al., 2001). In contrast, lighter females may not be able to wean their yearlings and reconceive after an inter-litter interval of only 2 years. Failure to reconceive can lead to extended maternal care, as in red deer (*Cervus elaphus*) (Clutton-Brock, Guinness, & Albon, 1983).

Our results suggest that large sample sizes may be required to detect the causes of variation in the duration of maternal care. Indeed, the direct effects of litter size and maternal mass

were only detected when considering both populations combined. However, whereas combining data from different populations increases sample size, it may conceal the importance of local factors. Indeed, we found marked differences in the causal mechanisms explaining variation in the duration of maternal care in the two populations, suggesting that environmental context matters. Reproductive rates and duration of maternal care can differ between populations of the same species with different access to resources and different environmental conditions (Borries et al., 2001; Lee, 1996; Lee et al., 1991; Nawaz, Swenson, & Zakaria, 2008).

In the North, yearling mass was the central determinant of the duration of maternal care, with lighter yearlings receiving longer maternal care. Maternal mass was also important and litter size had a marginal effect, but only indirectly through their effects on yearling mass; yearlings of lighter females and in larger litters received extended maternal care, because they were smaller. This result agrees with previous theoretical and empirical studies placing offspring mass as the central determinant of the duration of maternal care (Bowen et al., 2001; Dahle & Swenson, 2003a; König & Markl, 1987; Lee et al., 1991). In the North, climate harshness and lower food availability, suggested by overall smaller mass and slower growth rate of females (Zedrosser et al., 2006), may constrain females' energy allocation to reproduction. The cost-benefit ratio of extending maternal care may be higher, favouring terminating maternal care as soon as the yearlings are above a certain threshold mass (Dahle & Swenson, 2003a). In fact, extended maternal care seems to compensate for reduced cub growth in yearling brown bears, as mass of 2-year-olds in the North was similar, regardless of the duration of maternal care they had received (Dahle & Swenson, 2003a).

In the South, yearling mass, litter size, and maternal mass did not affect the duration of maternal care. Instead, the termination of maternal care may be driven by the prospects of survival gains for offspring (Balme et al., 2017). Yearling mortality is mostly due to

hunting and intra-specific killing in the South (R. Bischof, Swenson, Yoccoz, Mysterud, & Gimenez, 2009), and, thus, likely not related to their mass, although females appear more vulnerable to intra-specific killing (Swenson, Dahle, & Sandegren, 2001). By prolonging the period of maternal care, females can provide protection to yearlings from both conspecifics and hunters (Van de Walle et al., 2018). Combined with more favourable environmental conditions that may reduce the costs of longer maternal care in the South, this may explain why some females continue maternal care, regardless of yearling mass. Detecting cost of reproduction in the wild can be challenging (Hamel et al., 2010), potentially because life-history trade-offs are only apparent under limited resources (Stearns, 1989) and can be masked by individual heterogeneity in resources acquisition and allocation (van Noordwijk & de Jong, 1986).

Only maternal age directly influenced care duration in the South. Hunting regulations prohibit the killing of members of family groups in Sweden, giving a survival advantage to females providing longer maternal care (Van de Walle et al., 2018). Hunting-induced selectivity could thus explain why females providing longer maternal care were older; they survived longer. The relationship with maternal age may not apply to the North where hunting is mostly illegal or management-related and thus not restricted to non-members of family groups (Rauset et al., 2016; Swenson et al., 2017). Our results suggest that regulated hunting has the potential to influence the cost-benefit balance of durations of maternal care. This is in line with the growing evidence of human activities, e.g., over-exploitation, as the most important agent of trait change, affecting morphology, behaviour, and life histories of wild populations (Darimont et al., 2009; Law, 2000; Leclerc, Zedrosser, & Pelletier, 2017).

The variance explained by the fixed effects included in our models for the South was very low (7.8%), suggesting other, unmeasured factors may be important. Over the last ~30 years, the proportion of litters receiving 2.5 years of maternal care increasing from 0% prior to 1995 to about 25% since then (Van de Walle et al., 2018). In parallel, yearling and

maternal mass have recently declined in the population (Leclerc, Van de Walle, Zedrosser, Swenson, & Pelletier, 2016), suggesting they might be related and perhaps caused by increases in population density during the study period (Bischof et al., 2018; Swenson et al., 2017). However, the duration of maternal care was not affected by maternal nor yearling mass, i.e., traits on which density-dependence should act (Bonenfant et al., 2009). Nevertheless, based on a post hoc analysis using an index of local density, we found a direct link between density and maternal mass, but not between density and yearling mass or between density and the duration of maternal care (Appendix A3.3). Therefore, at higher local density, females are smaller, which results in smaller yearlings, but this does not seem to affect whether a female will continue maternal care or not. Another alternative explanation could be that females extend maternal care to match with periods of high food abundance (Balme et al., 2017; Grüebler & Naef-Daenzer, 2008). In the South, bilberry (*Vaccinium myrtillus*) is the most important food source for brown bears in the fall (Stenset et al., 2016). Based on a restricted dataset (10 years) comprising years when an index of annual bilberry production was estimated (Hertel et al., 2018), we found that food availability directly affected both maternal and yearling mass (Appendix A3.4). However, none of these variables were linked directly or indirectly to the duration of maternal care. Finally, a previous study in the South showed that the duration of maternal care may be constrained by sexual conflicts (Van de Walle et al., 2019), with males playing an important role in the termination of maternal care (Dahle & Swenson, 2003b), which has been reported in carnivores and primates (Elliot, Valeix, Macdonald, & Loveridge, 2014; Morino & Borries, 2017). Limitations in sample size, however, prevented us to account for male-female interactions in our path analyses.

The proportion of variance explained by maternal identity was much higher in the South (34.0%) than in the North (18.7%). In the North, females may change their reproductive tactic from one reproductive event to the next (Dahle & Swenson, 2003a), in response to changes in yearling condition. This contrasts with the South, where the duration of maternal

care is a repeatable trait, i.e., females tend to use the same tactic over time (Van de Walle et al., 2018).

In species with large variations in the duration of maternal care (e.g., one year in our study), the need to understand and identify the drivers of the duration of maternal care and its demographic consequences is obvious. However, small variations in this trait also can have measurable consequences for offspring fitness (Bowen et al., 2001). The termination of maternal care can also determine the timing of female availability for the next conception, which, in turn, may affect mate choice and have a downstream rippling effect over the events following in the reproductive cycle (Hogg, Dunn, Poissant, Pelletier, & Byers, 2017). Observing family break-up and documenting the end of maternal care in the wild is challenging, especially in species with large home ranges. However, data from long-term and individual-based studies on a large number of individuals are increasingly becoming available, which should help further disentangling the determinants of the duration of maternal care in wild animal populations.

3.7 Acknowledgments

We are grateful to all the people that have contributed to the data collection. Special thanks to Sven Brunberg and Andrea Friebe for their invaluable help with data collection, management and archiving. We thank Bill Shipley for his help with path analyses, and Shane Frank and Anne Hertel for providing data on bear density and berry indices. We also thank Marco Festa-Bianchet and Dany Garant for their constructive comments. We thank the Quebec Centre for Biodiversity Science. This is SBBRP scientific paper number XXX. J.V.d.W. and F.P. were funded by the Natural Sciences and Engineering Research Council of Canada (grant nos. PGSD2-504356-2017, CRSNG-355492, CRC-229221). The Scandinavian Brown Bear Research Project is funded by the Swedish Environmental

Protection Agency, the Norwegian Directorate for Nature Management and the Austrian Science Fund. This research is part of the NFR project 269863 BearConnect.

3.8 Authors' contributions

J.V.d.W., F.P. and A.Z. conceived and designed the study. A.Z. and J.E.S. coordinated the project and data collection. J.V.d.W. analysed the data and wrote the first draft. All authors contributed to the interpretation of the data and subsequent manuscript writing and revisions.

3.9 Data availability

Data for the analyses included in this manuscript will be deposited on Dryad upon acceptance of the manuscript.

3.10 References

Arnemo, J. M., Evans, A., & Fahlman, Å. (2011). *Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx.* Evenstad, Norway: Hedmark University College.

Balme, G. A., Robinson, H. S., Pitman, R. T., & Hunter, L. T. B. (2017). Flexibility in the duration of parental care: female leopards prioritise cub survival over reproductive output. *Journal of Animal Ecology*, *86*(5), 1224–1234. doi: 10.1111/1365-2656.12713

Barton, K. (2019). *MuMIn: Multi-Model Inference. R package version 1.43.6. https://CRAN.R-project.org/package=MuMIn*. Retrieved from https://cran.r-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi: 10.18637/jss.v067.i01

Bischof, R., Bonenfant, C., Rivrud, I. M., Zedrosser, A., Friebe, A., Coulson, T., … Swenson, J. E. (2018). Regulated hunting re-shapes the life history of brown bears. *Nature Ecology & Evolution, 2*(1), 116–123. doi: 10.1038/s41559-017-0400-7

Bischof, R., Swenson, J. E., Yoccoz, N. G., Mysterud, A., & Gimenez, O. (2009). The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology, 78*, 656–665. doi: 10.1111/j.1365-2656.2009.01524.x

Bonenfant, C., Gaillard, J.-M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., … Duncan, P. (2009). Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research, 41*, 313–357. doi: 10.1016/S0065-2504(09)00405-X

Borries, C., Koenig, A., & Winkler, P. (2001). Variation of life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology, 50*(5), 391–402. doi: 10.1007/s002650100391

Borries, C., Lu, A., Ossi-Lupo, K., Larney, E., & Koenig, A. (2014). The meaning of weaning in wild Phayre's leaf monkeys: last nipple contact, survival, and independence. *American Journal of Physical Anthropology, 154*(2), 291–301. doi: 10.1002/ajpa.22511

Bowen, W. D., Ellis, S. L., Iverson, S. J., & Boness, D. J. (2001). Maternal effects on offspring growth rate and weaning mass in harbour seals. *Canadian Journal of Zoology, 79*, 1088–1101. doi: 10.1139/cjz-79-6-1088

Bowen, W. D., Oftedal, O. T., & Boness, D. J. (1985). Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Canadian Journal of Zoology, 63*, 2841–2846. doi: 10.1139/z85-424

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach* (2nd editio). New York, NY: Springer-Verlag.

Charnov, E. L., & Ernest, S. K. M. (2006). The offspring-size/clutch-size trade-off in mammals. *American Naturalist, 167*(4), 578–582. doi: 10.1086/501141

Clutton-Brock, T. H. (1988). Reproductive success. In T. H. Clutton-Brock (Ed.), *Reproductive success: studies of individual variation in contrasting breeding systems.* Chicago: The University of Chicago Press.

Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, New Jersey: Princeton University Press.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1983). The costs of reproduction to red deer hinds. *Journal of Animal Ecology, 52*(2), 367–383. doi: 10.2307/4560

Dahle, B., & Swenson, J. E. (2003a). Factors influencing length of maternal care in brown bears *(Ursus arctos*) and its effect on offspring. *Behavioral Ecology and Sociobiology, 54*(4), 352–358. doi: 10.1007/s00265-003-0638-8

Dahle, B., & Swenson, J. E. (2003b). Family break-up in brown bears: are young forced to leave? *Journal of Mammalogy, 84*(2), 536–540. doi: 10.1644/1545-1542(2003)084<0536:FBIBBA>2.0.CO;2

Dahle, B., Zedrosser, A., & Swenson, J. E. (2006). Correlates with body size and mass in yearling brown bears (*Ursus arctos*). *Journal of Zoology, 269*, 273–283. doi: 10.1111/j.1469-7998.2006.00127.x

Darimont, C. T., Carlson, S. M., Kinnison, M. T., Paquet, P. C., Reimchen, T. E., & Wilmers, C. C. (2009). Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences*, *106*(3), 952–954. doi: 10.1073/pnas.0809235106

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology.* Oxford: Wiley-Blackwell.

Elliot, N. B., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos, 123*(9), 1049–1056. doi: 10.1111/oik.01266

Fairbanks, L. A., & McGuire, M. T. (1995). Maternal condition and the quality of maternal care in vervet monkeys. *Behaviour, 132*, 733–754. doi: 10.1016/S0065-3454(08)60343-5

Friebe, A., Evans, A. L., Arnemo, J. M., Blanc, S., Brunberg, S., Fleissner, G., … Zedrosser, A. (2014). Factors affecting date of implantation, parturition, and den entry estimated from activity and body temperature in free-ranging brown bears. *PLoS ONE, 9*(7), e101410. doi: 10.1371/journal.pone.0101410

Georges, J.-Y., & Guinet, C. (2000). Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology, 81*(2), 295–308. doi: 10.1890/0012-9658(2000)081[0295:MCITSF]2.0.CO;2

Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist, 28*(3), 863–875. doi: 10.1093/icb/28.3.863

Grüebler, M. U., & Naef-Daenzer, B. (2008). Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. *Ecology, 89*(10), 2736–2745. doi: 10.1890/07-0786.1

Hamel, S., Gaillard, J.-M., Yoccoz, N. G., Loison, A., Bonenfant, C., & Descamps, S. (2010). Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecology Letters, 13*, 915–935. doi: 10.1111/j.1461-0248.2010.01478.x

Hamilton, W. D. (1964). The genetical evolution of social behavior II. Journal of *Theoretical Biology, 7*, 17–52. doi: 10.1016/0022-5193(64)90039-6

Hertel, A. G., Bischof, R., Langval, O., Mysterud, A., Kindberg, J., Swenson, J. E., & Zedrosser, A. (2018). Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos, 127*(2), 197–207. doi: 10.1111/oik.04515

Hogg, J. T., Dunn, S. J., Poissant, J., Pelletier, F., & Byers, J. A. (2017). Capital vs. income-dependent optimal birth date in two North American ungulates. *Ecosphere, 8*(4), e01766. doi: 10.1002/ecs2.1766

König, B., & Markl, H. (1987). Maternal care in house mice: I. The weaning strategy as a means for parental manipulation of offspring quality. *Behavioral Ecology and Sociobiology, 20*(1), 1–9. doi: 10.1007/BF00292161

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science, 57*, 659–668. doi: 10.1006/jmsc.2000.0731

Leclerc, M., Van de Walle, J., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2016). Can hunting data be used to estimate unbiased population parameters? A case study on brown bears. *Biology Letters, 12*(6), 20160197. doi: 10.1098/rsbl.2016.0197

Leclerc, M., Zedrosser, A., & Pelletier, F. (2017). Harvesting as a potential selective pressure on behavioural traits. *Journal of Applied Ecology, 54*(6), 1941–1945. doi: 10.1111/1365-2664.12893

Lee, P. C. (1996). The meanings of weaning: growth, lactation, and life history. *Evolutionary Anthropology, 5*(3), 87–98. doi: 10.1002/(SICI)1520-6505(1996)5:3<87::AID-EVAN4>3.0.CO;2-T

Lee, P. C., Majluf, P., & Gordon, I. J. (1991). Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology, London, 225*(1), 99–114. doi: 10.1111/j.1469-7998.1991.tb03804.x

Lee, P. C., & Moss, C. J. (1986). Early maternal investment in male and female African elephant calves. *Behavioral Ecology and Sociobiology, 18*(5), 353–361. doi: 10.1007/BF00299666

Lonsdorf, E. V., Stanton, M. A., Pusey, A. E., & Murray, C. M. (2019). Sources of variation in weaned age among wild chimpanzees in Gombe National Park, Tanzania. *American Journal of Physical Anthropology*, 171(3):419-429. doi: 10.1002/ajpa.23986

Manchi, S., & Swenson, J. E. (2005). Denning behaviour of Scandinavian brown bears *Ursus arctos*. *Wildlife Biology, 11*(2), 123–132. doi: 10.2981/0909-6396(2005)11[123:DBOSBB]2.0.CO;2

Matson, G., Van Daele, L., Goodwin, E., Aumiller, L., Reynolds, H., & Hristienko, H. (1993). *A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth*. Milltown: Matson's Laboratory.

Morino, L., & Borries, C. (2017). Offspring loss after male change in wild siamangs: the importance of abrupt weaning and male care. *American Journal of Physical Anthropology, 162*(1), 180–185. doi: 10.1002/ajpa.23082

Morris, D. W. (1986). Proximate and ultimate controls on life-history variation: the evolution of litter size in white-footed mice (*Peromyscus leucopus*). *Evolution, 40*(1), 169–181. doi: 10.2307/2408614

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface, 14*, 20170213. doi: 10.1098/rsif.2017.0213

Nawaz, M. A., Swenson, J. E., & Zakaria, V. (2008). Pragmatic management increases a flagship species, the Himalayan brown bears, in Pakistan's Deosai National Park. *Biological Conservation, 141*, 2230–2241. doi: 10.1016/j.biocon.2008.06.012

Rauset, G. R., Andrén, H., Swenson, J. E., Samelius, G., Segerström, P., Zedrosser, A., & Persson, J. (2016). National parks in northern Sweden as refuges for illegal killing of large carnivores. *Conservation Letters, 9*(5), 334–341. doi: 10.1111/conl.12226

Schwartz, C. C., Miller, S. D., & Haroldson, M. A. (2003). Grizzly bear. In G. A. Feldhammer, B. C. Thompson, & J. A. Chapman (Eds.), *Wild mammals of North America: biology, management and conservation* (pp. 556–586). Baltimore, USA: The John Hopkins University Press.

Shipley, B. (2000). *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference.* Cambridge, UK: Cambridge University Press.

Shipley, B. (2013). The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology, 94*(3), 560–564. doi: 10.1890/12-0976.1

Smiseth, P. T., Kölliker, M., & Royle, N. J. (2012). What is parental care? In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care*. Oxford: Oxford University Press.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology, 3*, 259–268. doi: 10.2307/2389364

Stenset, N. E., Lutnæs, P. N., Bjarnadóttir, V., Dahle, B., Fossum, K. H., Jigsved, P., … Swenson, J. E. (2016). Seasonal and annual variation in the diet of brown bears *Ursus arctos* in the boreal forest of southcentral Sweden. *Wildlife Biology, 22*(3), 107–116. doi: 10.2981/wlb.00194

Steyaert, S. M. J. G., Endrestøl, A., Hackländer, K., Swenson, J. E., & Zedrosser, A. (2012). The mating system of the brown bear *Ursus arctos*. *Mammal Review, 42*(1), 12–34. doi: 10.1111/j.1365-2907.2011.00184.x

Swenson, J. E., Dahle, B., & Sandegren, F. (2001). Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus, 12*, 81–92.

Swenson, J. E., Schneider, M., Zedrosser, A., Söderberg, A., Franzén, R., & Kindberg, J. (2017). Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. *Wildlife Biology*, wlb.00251. doi: 10.2981/wlb.00251

Trillmich, F. (1986). Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephlus galapagoensis. Behavioral Ecology and Sociobiology, 19*(1980), 157–164. doi: 10.1007/BF00300855

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man*. Chicago, Illinois: Aldine Publishing Company.

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist, 14*(1), 249–264. doi: 10.1093/icb/14.1.249

Van de Walle, J., Leclerc, M., Steyaert, S. M. J. G., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2019). Proximity to humans is associated with longer maternal care in brown bears. *Behavioral Ecology and Sociobiology, 73*, 158. doi: 10.1007/s00265-019-2764-y

Van de Walle, J., Pigeon, G., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2018). Hunting regulation favors slow life histories in a large carnivore. *Nature Communications, 9*(1), 1100. doi: 10.1038/s41467-018-03506-3

van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist, 128*, 137–142. doi: 10.1086/284547

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist, 100*(916), 687–690. doi: 10.1086/282461

Winkler, D. W. (1987). A general model for parental care. *American Naturalist, 130*(4), 526–543. doi: 10.1086/284729

Zedrosser, A., Dahle, B., & Swenson, J. E. (2006). Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy, 87*(3), 510–518. doi: 10.1644/05-MAMM-A-218R1.1

CHAPITRE 4
LIEN ENTRE CONFLIT SEXUEL ET DURÉE DES SOINS MATERNELS

4.1 Description de l'article et contribution

Cet article traite d'un aspect généralement ignoré dans l'évaluation des facteurs pouvant influencer la durée des soins maternels; la divergence d'intérêts dans la reproduction entre les sexes et les conflits sexuels qui en résultent. Dans cet article, nous nous sommes basés sur le principe que, chez les mammifères, les mâles pourraient forcer la séparation hâtive des groupes familiaux et avons testé l'hypothèse selon laquelle les femelles ours brun éviteraient les mâles durant la période de reproduction pour limiter les risques de séparation avec leurs jeunes. Nous avons montré, qu'effectivement, les femelles ayant procuré une courte période de soins maternels sélectionnaient des habitats similaires aux mâles, alors que les femelles ayant procuré une longue période de soins maternels sélectionnaient des habitats différents des mâles, telle que la proximité aux habitations humaines. Les femelles ours brun pourraient ainsi tirer profit d'un paysage dominé par l'Homme afin de se protéger des mâles et moduler leurs tactiques de reproductions.

L'idée de cet article est inspirée des travaux de Sam MJG Steyaert sur l'infanticide sexuellement sélectionné chez l'ours brun. Je suis à l'origine de l'idée, que j'ai peaufinée avec l'aide de collaborations que j'ai initiées avec Sam MJG Steyaert et Martin Leclerc et de ma directrice, Fanie Pelletier. Sam MJG Steyaert a fourni les cartes d'habitat de la Suède. Martin Leclerc a extrait les localisations GPS et les variables d'habitat. J'ai réalisé les analyses statistiques suivant les conseils de Martin Leclerc. J'ai écrit la première version de l'article et tous les auteurs ont contribué aux versions subséquentes. Andreas Zedrosser et Jon E Swenson ont coordonné le SBBRP. DOI : 10.1007/s00265-019-2764-y.

Proximity to humans is associated with longer maternal care in brown bears

Behavioral Ecology and Sociobiology (2019), 73 :158

Joanie Van de Walle, Martin Leclerc, Sam M.J.G. Steyaert, Andreas Zedrosser, Jon E. Swenson, et Fanie Pelletier

https://doi.org/10.1007/s00265-019-2764-y

4.2 Abstract

In the sexual conflict over the duration of maternal care, male mammals may improve their reproductive success by forcing early mother-offspring separation in species where lactation supresses estrus. However, when individual females benefit from continuing to care for their current offspring, they should adopt counter-strategies to avoid separation from offspring. Here, we tested whether spatial segregation from adult males and proximity to humans during the mating season could be associated with longer maternal care in the Scandinavian brown bear (*Ursus arctos*). Using Resource Selection Functions (RSFs), we contrasted habitat selection patterns of adult males and those of adult females with yearlings that either provided 1.5 years of maternal care ("short-care females") or continued care for an additional year ("long-care females") during the mating season, the period when family break-ups typically occur. Males and short-care females had similar habitat selection patterns during the mating season. In contrast, habitat selection patterns differed between males and long-care females, suggesting spatial segregation between the two groups. In particular, long-care females used areas closer to human habitations compared to random locations (defined here as selection), whereas males used areas further to human habitations compared to random locations (defined here as avoidance). Our results show a correlation between habitat selection behavior and the duration of maternal care. We suggest that proximity to humans during the mating season may represent a female tactic to avoid adverse interactions with males that may lead to early weaning of offspring.

4.3 Significance statement

In mammalian species where lactation supresses ovulation, males may gain a reproductive advantage by forcing early mother-offspring separation, however females can respond through behavioral tactics. We show that female brown bears with yearling cubs can spatially segregate from males during the mating season and that this behavior is associated with longer maternal care. Females selecting areas close to human habitations tend to keep their yearlings for an additional year, suggesting that human presence could have a shielding effect from males. Our study is among the few to explore sexual conflicts over the duration of maternal care close to weaning and shows that animals have the potential to adjust their behavioral tactics to make use of human-dominated landscapes.

Keywords: Sexual conflict, maternal care, spatial segregation, brown bear.

4.4 Introduction

Interest in reproduction differs between the sexes, mainly in terms of number of mating opportunities, leading to sexual conflicts (Arnqvist and Rowe 2005). Sexual traits favoring the interests of one sex will be under selective pressure, sometimes at the expense of the other sex. However, the evolution of sexual traits is not independent between the sexes (Chapman et al. 2003; Arnqvist and Rowe 2005). Indeed, the sex incurring the costs imposed by a behavior of the other sex may respond by adopting counter-strategies (Lessels 2012). For example, female European starlings (*Sturnus vulgaris*) coerce males into providing more parental investment by preventing them from mating with other females (Sandell and Smith 1996). In biparental care systems, the level of care provided by each parent is a common source of sexual conflicts, with several examples across birds and mammals (Arnqvist and Rowe 2005).

Parental care and its duration can limit reproductive opportunities for both sexes, leading to a sexual conflict over the duration of those care, even in species where care is provided by one sex only. Yet, this type of conflict has received little attention. In 90% of mammals, females are the sole providers of parental care (Clutton-Brock 1991). During the period of maternal care, lactation can hormonally supress estrus (Spady et al. 2007), leaving females unavailable for mating and to produce and/or care for new offspring (Tarwater and Brawn 2010; Balme et al. 2017). Early separation from offspring can thus allow females to mate again rapidly, increasing their reproductive success. Because continued maternal care implies a loss of reproductive opportunities for females, it follows that it should be provided only as long as the net benefits exceed the benefits accrued from future reproduction (Williams 1966). However, longer maternal care can be beneficial under some circumstances, as flexibility in the duration of maternal care is observed in several mammalian species (Lee et al. 1991). Despite our limited knowledge of the factors influencing the duration of maternal care and the dynamics of mother-offspring separation

(including mother-offspring conflict; Trivers 1974), there is a general tendency across mammals for females to wean offspring once the latter have reached a critical body mass (Lee et al. 1991). Females rearing smaller offspring tend to prolong maternal care (Lee et al. 1991; Dahle and Swenson 2003a) to improve the survival prospects of their progeny. Delayed dispersal of offspring can be favored when dispersal success is low (Boyce 1981) and maternal care can be extended to buffer the effect of adverse environmental conditions (Grüebler and Naef-Daenzer 2008). For example, some female leopards (*Panthera pardus*) continue care of cubs during periods of prey scarcity, which greatly improves their survival chances (Balme et al. 2017). In brown bears (*Ursus arctos*), although short maternal care improves reproductive success of females, the gain in current offspring survival from continued maternal care can compensate for reduced reproductive opportunities, leading to similar fitness output for short- and long-caring females (Van de Walle et al. 2018). The reproductive success of males, however, is affected almost exclusively by the number of successful copulations they can achieve (Bateman 1948). Thus, because continued maternal care reduces female availability for reproduction, it likely has a greater effect on the reproductive success of males, compared to that of females. Most importantly, longer maternal care reduces the number of females available for reproduction at the population level, with potential consequences for the operational sex ratio and selection on male sexual behaviors (Shuster and Wade 2003).

Males may improve their reproductive success by shortening the duration of maternal care, thereby inducing estrus in females (Lessels 1999). This scenario gives rise to an extreme form of sexual conflict, sexually selected infanticide (SSI), where a male kills unrelated offspring to then mate with the victimized female (Hrdy 1979; Lukas and Huchard 2014). For example, when male African lions (*Panthera leo*) take over a new pride, they typically kill the dependent cubs, after which the victimized mothers rapidly enter estrus and mate with the perpetrators (Loveridge et al. 2007). SSI has been shown to efficiently shorten inter-birth intervals in several carnivores and primates (Smuts and Smuts 1993; Bellemain et al. 2006; Zhao et al. 2011; Balme and Hunter 2013). There are other mechanisms

allowing males to shorten inter-birth intervals, without directly killing dependent offspring. For instance, males may force the early termination of maternal care by inducing either abortion or early weaning of offspring (Bruce 1959; Elliot et al. 2014). In lions, males taking over a pride also force the premature dispersal of cubs that would have otherwise received several additional months of maternal care (Elliot et al. 2014). Male-induced separation of mother and offspring may be an important mechanism for males to acquire mating opportunities (Dahle and Swenson 2003b), especially when offspring are older and harder to kill.

Counter-strategies can be adopted by females to avoid adverse interactions with males (Agrell et al. 1998). For example, spatial segregation from males is a tactic employed by females with young to avoid the risk of aggressive encounters in several species (e.g. Smultea 1994, Ben-David et al. 2004, Martin and da Silva 2004, Libal et al. 2011). In brown bears, female with cubs-of-the-year can alter their habitat and daybed selection patterns (Suring et al. 2007; Steyaert et al. 2013a; Elfström et al. 2014b; Skuban et al. 2018) to avoid dominant adult males during the spring and early summer, i.e. the period of high risk for sexually selected infanticide (Gosselin et al. 2017). In some populations, females even have been reported to use human presence as a shelter against males (Steyaert et al. 2016; Skuban et al. 2018). However, studies on spatial segregation from males have mainly focused on the period when females are accompanied by cubs-of-the-year. Whether females can also use this counter-strategy when with older offspring to avoid early weaning, i.e., if spatial segregation from males could favor continued maternal care, remains unknown.

Compared to gestation time (0.5 years; Steyaert et al. 2012), the period of maternal care is long in brown bears (between 1.5 and 2.5 years in Sweden; Dahle and Swenson 2003a). Despite reducing reproductive rates, longer maternal care has been associated with improved survival prospects for both adult females and yearlings (i.e. 1 year-old cubs) in

Sweden, due to a hunting regulation protecting family groups. The gain in survival from longer maternal care can compensate for reduced reproductive success in this population, and both maternal care tactics (short- and long-care females) yield similar fitness output under average hunting pressure (Van de Walle et al. 2018). However, longer maternal care can limit male reproductive opportunities, because females in lactational anestrus will not mate until they have separated from their current litter (Dahle and Swenson 2003b; Spady et al. 2007). Therefore, a female providing 2.5 years of maternal care will be available for mating only once every three years. In contrast, a female that separates from her offspring after 1.5 years of maternal care will be available for mating one year earlier. Because females may re-enter estrus after 2-7 days following cub loss during the mating season (Bellemain et al. 2006; Steyaert et al. 2012, 2014), there should be strong incentive for males to force the separation of females from yearling offspring to gain mating opportunities. Killing of yearlings by males has been reported, but whether this behavior is sexually selected has not been investigated (Swenson et al. 2001). However, in most documented cases of family break-ups, males were observed in the vicinity (Dahle and Swenson 2003b). This suggests that males may play a role in the termination of maternal care, such as inducing early weaning.

Our main objective was to evaluate whether females with yearlings spatially segregate from males during the mating season and if this behavior is associated with longer maternal care. We contrasted habitat selection behavior of adult (≥ 5 years-old) males with that of adult females with dependent yearlings during the mating season. Females with yearlings were classified according to whether they had provided 1.5 years of maternal care (hereafter termed "short-care females") or continued maternal care for an additional year (hereafter termed "long-care females"). We focused on the period from den emergence until the season of family break-up, which also corresponds to the mating season. First, because of the potential role of males in the termination of maternal care (Dahle and Swenson 2003b), we predicted that short-care females would show a habitat selection behavior similar to males during the mating season. Second, we predicted that long-care females would use

different habitats than males during the mating season. Third, in line with previous work showing that females with cubs-of-the-year can use human presence as a shield against males (Steyaert et al. 2016), we further predicted that long-care females would use habitats closer to human presence.

4.5 Methods

4.5.1 Study area

The study area is located in south-central Sweden (approximately 61° N, 15° E) and encompasses approximately 13,000 km^2 of rolling landscape dominated by intensively managed forests of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula* spp.). Age of forest stands ranges from recent clear-cuts to old plantations (90-100 years). Apart from forest stands, the landscape is also largely composed of bogs and lakes. Elevation ranges from 150-810 m asl. The landscape is dominated by human presence, with a dense network of gravel and paved roads used for forestry activities (0.7 km/km^2) and access to private properties (0.3 km/km^2). There are few main public roads with high-traffic volume (0.14 km/km^2) in the area (Steyaert et al. 2016). Apart from small villages (≥ 200 inhabitants) in the north and in the south, the study area contains only small settlements (< 200 inhabitants) and recreational cabins distributed rather homogeneously throughout (Steyaert et al. 2016). Brown bear population density was estimated in 2002 at 20 bears/1000 km^2 in the area (Solberg et al. 2006). Hunting of bears is allowed throughout the study area in the fall and hunters can shoot any bear, regardless of age or sex, except members of family groups (females with their dependent cubs of any age).

4.5.2 Animal captures and monitoring

As part of an individual-based, long-term monitoring program in south-central Sweden, bears are captured in the spring soon after den emergence (late April) from a helicopter by darting (Dan-Inject, Børkop, Denmark) with an immobilizing drug. Captured bears are equipped with a GPS collar (GPS Plus; Vectronic Aerospace, Germany). We located collared females and counted their cubs from the ground or a helicopter a minimum of three times during the non-denning period: at den emergence, after the mating season and before den entry. We captured collared females and their yearlings. At this time, we weighed all the bears and determined the sex of the yearlings. Yearlings were not GPS-collared, because of their rapid growth. Instead, yearlings were equipped with a VHF transmitter (Telonics, model IMP/400/L HC) implanted in the peritoneal cavity. Although the monitoring of females is the primary objective of the program, males were also monitored, but more opportunistically. Most bears were captured as yearlings with their respective family groups and consequently their year of birth was known. For bears not followed from birth, a premolar tooth was extracted for age determination (Matson et al. 1993). See Arnemo et al. (2011) for further details on capture and handling. All captures and handling were approved by the appropriate authority and ethical committee (Djuretiska nämden i Uppsala, Sweden). Because our study involved focal animals, it was not possible to record data blind.

4.5.3 Spatial and statistical analyses

The GPS collars were programed to deliver a position every 1 hour. We removed positions with dilution of precision > 10 to improve spatial accuracy (Lewis et al. 2007). GPS data were collected during the period between den emergence and family break-up for the three classes of bears (i.e. males, long-care females, and short-care females), but for long-care

females and short-care females, we only used the year they were accompanied by yearlings in our analyses (Figure 4.1). For every bear-year, we considered the date of den emergence as the first date when available GPS data showed movements away from the denning site. For short-care females, we considered that family break-up occurred between the last date the female was observed with her yearlings and the first date the female was observed alone. However, because females show drastic and rapid changes in behavior and movement patterns after separating with cubs (Steyaert et al. 2014), we only used GPS relocations until the date of the last observation of the female with her yearlings, which represents a conservative date of family break-up. To keep the period during which we collected GPS data and assessed habitat selection of long-care females, short-care females, and adult males comparable, we randomly assigned an end date for each long-care female and adult male according to the density distribution of family break-ups obtained for short-care females (Appendix 4.1: Table A4.1). We contrasted habitat selection of males, long-care females, and short-care females using a resource selection approach, where GPS locations represented resource use and random locations represented resource availability (Lele et al. 2013). For every bear-year, we evaluated home range as a 100% minimum convex polygon (Mohr 1947). Availability was determined by drawing a random sample of locations within the home range in equal number to the GPS locations recorded for every bear-year (third order of selection; sensu Johnson 1980). We extracted land cover types (old-forest, mid-aged forest, young forest, clear-cut and bogs) and distance to human footprint (road, human habitation) variables known or expected to affect the probability of occurrence of males and females with dependent cubs (Steyaert et al. 2013a, 2016). For land cover type variables, we reclassified the Swedish land cover map (Svenska Marktäckedata, © Naturvårdsverket 2014) into water, bog, clear-cut, young forest (tree height < 7 m, >7 years old), mid-aged forest (tree height 7-15 m), old forest (tree height >15 m), and updated the maps annually for new clear-cuts, based on logging data obtained from the Swedish Forestry Agency (www.skogsstyrelsen.se). We used the Swedish National Road Database from the Swedish Transport Administration (© Trafikverket) to extract distance to the nearest road. We updated the road network annually by digitizing new logging roads, based on satellite image mosaics obtained from the Swedish Mapping,

Cadastral and Land Registration Authority (© Lantmäteriet). Because of image quality and availability, the years 2006, 2015, and 2016 were not updated. For those years, we used the maps that were closest in time to the GPS data for extraction. We used the Real Property Register from the Swedish Mapping, Cadastral and Land Registration Authority (© Lantmäteriet) to extract Eucledian distance to the nearest human habitation, annually updated for new buildings. Human habitations are found at various distances in the home ranges of all individuals from the two female groups (Appendix 4.1: Figure A4.1).

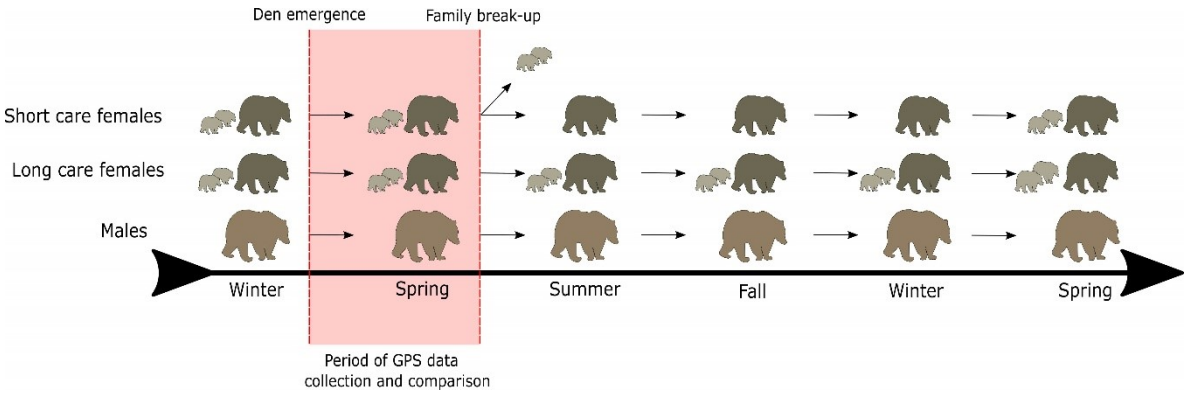

Figure 4.1 **Timeline showing that GPS data used to compare habitat selection between brown bear short-care females, long-care females and males were collected between den emergence and family break-up (red shaded area) in south-central Sweden.**

Females from the two groups were all accompanied by yearlings during this period.

4.5.4 Resource selection at the population level

We used logistic generalized linear mixed effects models (R package "lme4"; Bates et al. 2015) to estimate resource selection functions and habitat selection coefficients (Johnson et al. 2006; Lele et al. 2013). We compared resource use with resource availability and we defined the use of a resource in a larger proportion compared to its availability as selection, and the use of a resource in a lesser proportion compared to its availability as avoidance (Lele et al. 2013). Resource use (coded "1") and resource availability (coded "0") were set as the response variable, bear-year nested in bear identity as a random intercept, and distance to human footprint (roads, habitations) and land cover types (old-forest, mid-aged forest, young forest, clear-cut and bogs) as fixed effects. Land cover types were included as dummy variables (Boyce et al. 2002) and continuous "distance to" variables were scaled prior to analysis. Water was not included as a potential land cover type in our models. Also, due to variance inflation issues in our complete model, we removed one forest-type variable. Removing young forest resulted in a better model fit (lower Akaike Information Criterion, AIC), compared to model without old forest and model without mid-aged forest by 76.0 and 143.3, respectively. Therefore, we decided to remove young forest from our analysis, which resulted in a model with 4 land cover types ("mid-aged forest", "old forest", "clear-cut" and "bog"). We constructed three biologically plausible models to determine the relative importance of the human footprint and land cover type variables to explain resource selection by bears and three additional models using the same effect structure, but adding an interaction term with "group" (3 levels factor: "male", "long-care female", "short-care female") to each fixed effect (Table 4.1). Adding the interaction term allowed testing the importance of between-group differences in resource selection. Model selection was based on AIC and AIC weights (AIC_{wi}). We reversed the signs of coefficients of selection related to "distance to" variables for ease of interpretation. As a proxy for relative differences in habitat selection between the three groups, we calculated the sum of absolute differences in the coefficient of selection for each variable tested between males and long-care females, males and short-care females, and the two female groups. Large

values would indicate large overall dissimilarities, whereas small values would indicate similarities in habitat selection patterns. Following Steyaert et al. (2016), we quantified the relative importance of each variable in explaining between-group differences in resource selection by removing one interaction term at a time from the best performing model and compared AIC between the reduced model and the best performing model. All Variance Inflated Factors (VIF) were < 3 (Zuur et al. 2009).

4.5.5 Resource selection at the individual level

Although some habitats may be selected or avoided at the "population" or "group" level, variation between individuals within the same group is also expected (Leclerc et al. 2016). To assess the possibility that some individuals may have a disproportional effect on the population-level effect, we also modelled resource selection at the individual level (1 model per bear-year). We used generalized linear models, with the same fixed effect structure as the model selected in the first step, however excluding the interaction terms. Individual selection coefficients were extracted for the 6 variables included in the model. To test the effect of bear group on individual habitat selection patterns, we used a non-parametric multivariate analysis of variance. This approach, based on the comparison of between and among group distances in a multivariate space, allows for a lack of dependence on assumptions about data distribution (Anderson 2001). Individual selection coefficients were put into matrix format (rows = bear-year, columns = coefficient of selection for the 6 variables) and then converted into an Euclidean distance matrix. The distance matrix was used as a response variable in a permutational multivariate analysis of variance (PERMANOVA); with 1000 permutations (Anderson 2001) with the R package "vegan" (Oksanen et al. 2017). We also conducted *post-hoc* pairwise comparisons between the groups by performing multiple PERMANOVAS and applying a Bonferroni correction to adjust P-values (Anderson 2001).

4.6 Results

From 2004 to 2016, we obtained GPS positions for 78 bear-years: 52 male bear-years (23 individual males) and 26 bear-years for females with yearlings (from 16 individual females; Appendix 4.1: Table A4.1). We divided female data according to whether or not they became separated from their yearlings in that year, i.e. "short-care females" (14 bear-years from 11 individual females) or kept their yearlings for an additional year, i.e. "long-care females" (12 bear-years from 8 individual females). The two female groups did not differ significantly in terms of age (long-care females: mean = 12.1 years, short-care females: mean = 10.9 years, t = -0.91, df = 24, P = 0.37) or years of GPS data collection (long-care females: mean = 2011, short-care females: mean = 2010, t = -1.27, df = 24, P = 0.22), which suggests that age or temporal effects are not likely to confound the results.

Table 4.1 Candidate models to evaluate habitat selection of Scandinavian brown bears in south-central Sweden, 2004-2016.

Model	Model description	K	ΔAIC	AICw_i
1	Distance to road + Distance to habitation	5	1887.01	0
2	Mid-aged forest + Old forest + Bog + Clear-cut	7	966.40	0
3	Model 1 + Model 2	9	914.20	0
4	Model 1*Group	11	1102.27	0
5	Model 2*Group	17	813.57	0
6	**Model 4 + Model 5**	**23**	**0.00**	**1**

All models are logistic regressions with the binomial response variable "used/available" (used=1, available=0) and include bear-year nested in bear identity as a random intercept. When present, the interaction (indicated by a *) term "group" (3 levels variable: "male", "short-care female" and "long-care female") is applied to all variables within the model. Models are listed with their number of parameters (K), the difference in AIC to the best performing model (ΔAIC), and model weight (AICw_i).

4.6.1 Resource selection at the population level

The best performing model to explain bear resource selection included the interaction term "group" with "distance to" and land cover type variables (Table 4.1). Based on parameter estimates from the model (Table 4.2), we calculated the selection coefficient associated with each variable for the three bear groups separately. All bear groups avoided old forests (Figure 4.2a; Appendix 4.1: Table A4.2). Males and short-care females showed very similar avoidance of mid-aged forest, old forests, and bogs. In contrast, long-care females and males only showed similar selection coefficients for distance to roads and old forest, but the confidence intervals overlapped only very slightly. The sum of absolute differences in selection coefficients for all variables (our proxy of relative differences in habitat selection between the groups) was greatest between males and long-care females (males *vs* long-care females: 2.23, males *vs* short-care females: 1.08, long-care females *vs* short-care females: 1.20), suggesting that males and long-care females have the most contrasted habitat selection patterns. Long-care females showed selection coefficients for distance to human habitations and bogs that strongly diverged from males and short-care females (Figure 4.2a). With the exception of old forest, removing the interaction of all other variables in the selected model with "group" increased AIC values of the reduced models (all $\Delta AIC > 3$; Figure 4.2b). Removing the interaction between "habitation" and "group" substantially reduced model fit ($\Delta AIC = 670$), to a greater extent compared to any other variable (all other $\Delta AIC < 76$; Figure 4.2b), suggesting that between-group differences in probability of occurrence were mostly explained by distance to human habitations.

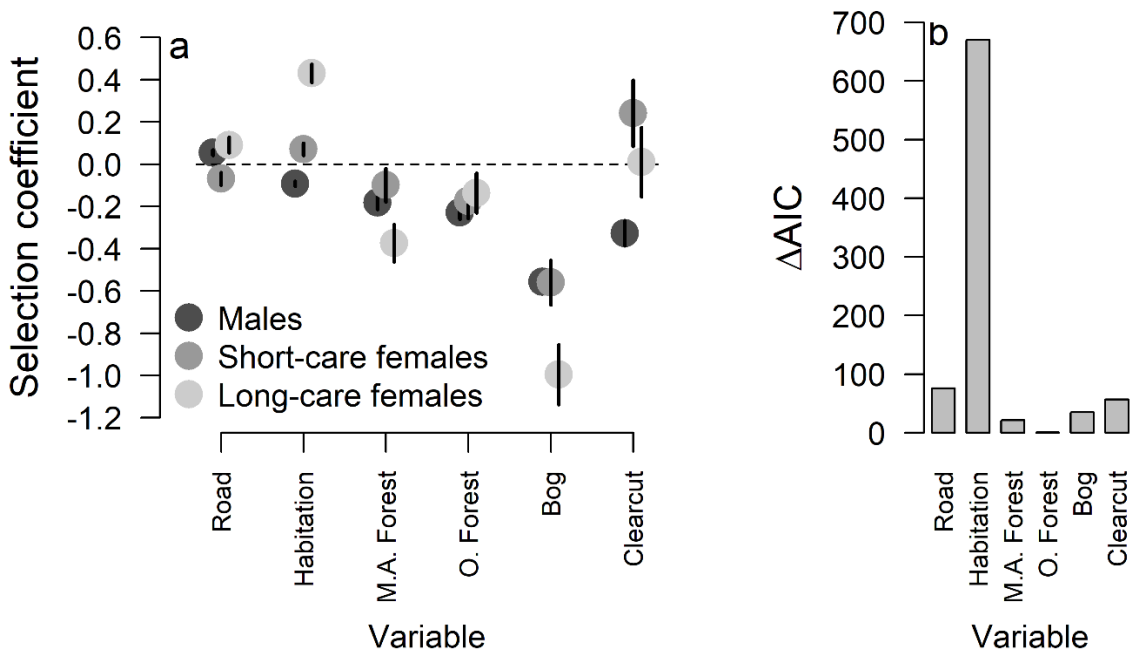

Figure 4.2 **Contrasted habitat selection coefficients (and 95% confidence intervals) between adult males, females separating from their yearlings ("short-care females") and females keeping their yearlings for an additional year ("long-care females") for brown bears during the mating season in south-central Sweden, 2004-2016 (a). For each variable tested in the global model, change in AIC after the removal of its interaction with the variable "group" (3 levels variable: "male", "short-care female" and "long-care female") for each variable in the best performing model explaining resource selection (b).**

Positive coefficients ($\beta > 0$) indicate that resources are used in a larger proportion compared to their availability (defined as selection), negative coefficients ($\beta < 0$) indicate that resources are used in a lesser proportion compared to their availability (defined as avoidance), and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to their availability. The signs of "distance to" variables were reversed for ease of interpretation. Large ΔAIC values suggest large

between-group differences in resource selection for the variables tested. Definitions: “Road” = distance to the nearest road, “Habitation” = distance to the nearest human habitation, “M.A.Forest” = mid-aged forest, “O.Forest” = old forest, “Bog” = bogs and tree-rich bogs, “Clearcut” = recently cut forest stand.

4.6.2 Resource selection at the individual level

For four bear-years (1 long-care female and 3 short-care females), the model did not converge, which hindered the proper estimation of individual selection coefficients. We thus removed those bear-years and extracted selection coefficients for the 74 remaining bear-years (52 males, 11 long-care females, and 11 short-care females) to perform the analysis. The three groups differed significantly in their habitat selection patterns (PERMANOVA, $F = 2.66$, $R^2 = 0.07$, $P = 0.02$), indicating more dissimilarities between groups than within groups. *Post-hoc* pairwise comparisons showed that only males and long-care females were statistically dissimilar in their habitat selection patterns (males vs long-care females: $F = 4.38$, $P_{adj} = 0.02$; males vs short-care females: $F = 1.63$, $P_{adj} = 0.47$; long-care females and short-care females: $F = 1.24$, $P_{adj} = 0.77$).

Table 4.2 **Parameter estimates (β) of the most parsimonious model to determine resource selection of brown bears males, females that have separated from their yearlings ("short-care female") and females keeping their yearlings for an additional year ("long-care female") in south-central Sweden, 2004-2016.**

		95% CI	
Model term	β	Lower	Upper
Intercept	0.19	0.15	0.23
Long-care female	-0.08	-0.16	0.01
Short-care female	-0.06	-0.14	0.02
Distance to the nearest road	0.05	0.04	0.07
Distance to the nearest habitation	-0.09	-0.11	-0.08
Old forest (1 vs 0)	-0.23	-0.26	-0.20
Mid-aged forest (1 vs 0)	-0.18	-0.21	-0.15
Bog (1 vs 0)	-0.56	-0.60	-0.51
Clearcut (1 vs 0)	-0.33	-0.39	-0.27
Long-care female * Distance to the nearest road	0.04	0.00	0.07
Short-care female * Distance to the nearest road	-0.12	-0.15	-0.09
Long-care female * Distance to the nearest habitation	0.52	0.48	0.57
Short-care female * Distance to the nearest habitation	0.16	0.13	0.19
Long-care female * Old forest (1 vs 0)	0.09	0.00	0.19
Short-care female * Old forest (1 vs 0)	0.05	-0.03	0.14
Long-care female * Mid-aged forest (1 vs 0)	-0.19	-0.28	-0.10
Short-care female * Mid-aged forest (1 vs 0)	0.08	0.00	0.16
Long-care female * Bog (1 vs 0)	-0.44	-0.58	-0.30
Short-care female * Bog (1 vs 0)	0.00	-0.11	0.10
Long-care female * Clearcut (1 vs 0)	0.34	0.17	0.50
Short-care female * Clearcut (1 vs 0)	0.57	0.41	0.73

Continuous variables were scaled. The signs of β coefficients for "distance to" variables were reversed for ease of interpretation. Positive coefficients ($\beta > 0$) indicate that resources are used in a larger proportion compared to their availability (defined here as selection), negative coefficients ($\beta < 0$) indicate that resources are used in a lesser proportion compared to their availability (defined here as avoidance), and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to availability.

4.7 Discussion

Identifying the factors influencing the termination of parental care has interested evolutionary ecologists for decades (Trivers 1972; Martin 1984; Lee et al. 1991). However, data on the timing of weaning are rarely available in wild populations. In this study, we tested whether female brown bears with yearlings could spatially segregate from dominant adult males during the mating season, and if this behavior was associated with longer maternal care. Females that provided short maternal care selected for habitats similar to those selected by males. In contrast, we found significant differences in habitat selection patterns between males and females that kept their yearlings for an additional year. The most striking difference was that long-care females strongly selected for human habitations, whereas males avoided human habitations. We hypothesize that by reducing the probability of encounters with males, spatial segregation from males through spatial association of females with humans may allow for continued maternal care in brown bears.

Our results showed that short-care females selected habitats similar to those selected by males during the mating season. Females could intentionally seek male habitats to initiate family break-up and secure mating, which would increase their reproductive success. The time distributions of family break-ups and the mating season overlap highly in brown bears (Craighead et al. 1995; Dahle and Swenson 2003b). During this period, there is a high risk of encounters with adult males because males cover considerable distances to gain mating opportunities (Dahle and Swenson 2003c), and females can associate with a large number of males (Steyaert et al. 2012). Encounters with males are also likely to result in mating as 82% of the short-care females included in our study that survived until the next year (n = 11) gave birth to a new litter, indicating that they encountered and mated with at least one male during the mating season.

Alternatively, unintentional selection of male habitats could increase the probability of encounters with males, which could lead to the separation of the family group. For many species, we know very little about male-female interactions around the time offspring are weaned. Direct observations in the wild are needed to confirm the respective roles of males and females in the termination of maternal care. However, we know that males pose a threat to yearlings in brown bears (Swenson et al. 2001). Because of sexual dimorphism in this species (Swenson et al. 2007; Steyaert et al. 2012), there is a risk of injuries and death associated with aggressive encounters with males (McLellan 1994; Craighead et al. 1995). The risk of SSI is usually considered to be only applicable for young offspring (Hrdy 1979). Yet, whether it is sexually selected or not, intraspecific killing by males is an important cause of mortality for brown bear yearlings (McLellan 1994; Swenson et al. 2001; Bischof et al. 2009). Swenson et al. (2001) estimated annual mortality of yearlings due to intraspecific killing by males at between 3-16% in south-central Sweden, suggesting that adult males pose a significant threat to yearlings. The cause of yearling killing by males remains unclear, but considering the significance of this threat, we suggest that an encounter with males should lead females to adopt risk minimizing tactics and be more prone to chase the yearlings away to minimize risk. In several primate species where males pose a threat to offspring, the arrival of a new male in a group has been associated with abrupt weaning and/or maternal rejection, irrespective of the age of the infant and even in the absence of aggressions (Fairbanks and McGuire 1987; Zhao et al. 2011; Morino and Borries 2017). For instance, in captive vervet monkeys (*Cercopithecus aethiops sabaeu*), females placed with a new male reject their infant more frequently near the expected weaning age, even without being harassed, compared to when placed with a resident male (Fairbanks and McGuire 1987).

We documented spatial segregation between brown bear females that kept their yearlings for an additional year and adult males during the mating season, both at the group and the individual levels. Whether the selection of habitats different than those of adult males arises from an active female-based decision to continue maternal care is difficult to ascertain.

Habitat selection patterns may vary according to differences in physiology, energy needs, and individual preferences (Main et al. 1996; Leclerc et al. 2016; Hertel et al. 2019) and these factors could explain why short-care females select habitats similar to those of males, whereas long-care females do not. We also hypothesize that such segregation by long-care females represents a risk-minimizing tactic of male-avoidance. To avoid interactions with dominant conspecifics, the most vulnerable individuals (usually sub-adults and females with dependent offspring) can adopt spatial avoidance as a risk-minimizing tactic (Hrdy 1979; Elfström et al. 2014b). By selecting different habitats than males, females may avoid risky encounters that could lead to either offspring mortality or separation. Spatial segregation from males by females with dependent offspring is a tactic commonly found in other mammalian species where males are a threat to offspring and females (Hrdy 1979; Smultea 1994; Martin and da Silva 2004; Rode et al. 2006; Loseto et al. 2006). Our results are also in line with previous studies on brown bears, showing that spatial segregation of females with cubs-of-the-year (the most vulnerable group to SSI) from adult males during the mating season can be a female tactic to reduce the risk of cub mortality and mitigate sexual conflict (Steyaert et al. 2013a, 2016). Here, we build upon this previous result and show that females with yearlings can also segregate spatially from males and that this segregation is associated with a higher probability of keeping the yearlings for an additional year. However, the correlative nature of our results does not allow us to infer causation.

Distance to human habitations was the most important factor explaining differences in habitat selection patterns between bear groups, with long-care females strongly selecting proximity to human habitations and adult males showing the opposite pattern. In Sweden, food-search does not explain the occurrence of brown bears close to human habitations as bears near human settlements do not have a superior diet than those in remote areas (Elfström et al. 2014a). Therefore, we do not think that long-care females select areas close to human habitations to access food. Also, it has been shown that continued maternal care compensates for lower offspring mass (Lee et al. 1991; Dahle and Swenson 2003a) in several mammals, such as brown bears. It could thus be argued that the distinct habitat

selection pattern of long-care females results from females selecting for higher quality habitats to obtain high-energy foods to increase offspring mass. However, in our study, mean yearling mass was comparable between litters of long-care females (mean = 18.8 kg, SD = 4.0, n = 11) and short-care females (mean = 16.4 kg, SD = 5.1; t = -1.23, df = 22, P = 0.23, n = 13).

According to the despotic distribution hypothesis (Fretwell and Lucas 1969), the most vulnerable individuals may be forced into suboptimal habitats. In brown bears, sexual segregation from dominant adult males by vulnerable females with young can entail a risk in terms of nutrition (Steyaert et al. 2013b) and disturbance by humans (Rode et al. 2006). Hunting is the main cause of mortality for brown bears in Sweden, affecting their natural mortality patterns, life histories, and behaviors (Ordiz et al. 2012; Zedrosser et al. 2013; Bischof et al. 2018; Van de Walle et al. 2018). Because of this and considering the importance of other human-related sources of mortality in brown bears (Bischof et al. 2009), humans can be perceived as a threat, which could explain why brown bears generally avoid human activity (Støen et al. 2015). However, there is a tendency for young individuals and females with cubs to come closer to human settlements than solitary adult females and adult males (Steyaert et al. 2013a; Elfström et al. 2014b; Skuban et al. 2018), which is interpreted as a safety-search tactic (Elfström et al. 2014b). For females with offspring, the risk of living in close proximity to humans appears to be outweighed by its fitness benefits. Indeed, cub survival is improved when Scandinavian brown bear females with cubs-of-the-year employ such a safety-search tactic and use humans habitations as shields against males (Steyaert et al. 2016). Moreover, females can alter their habitat selection behavior post-mating, allowing for a compensation of the nutritive cost of living in proximity to human habitations during the mating season (Steyaert et al. 2013b).

We propose that some females actively decide to avoid males during the mating season when accompanied by yearling offspring to avoid early family break-up. Accordingly, the

following year, when they will separate from their 2-year-olds (maternal care does not exceed 2.5 years in this population; Dahle and Swenson 2003a) they would then alter their habitat selection pattern towards adult male habitats to initiate family break-up. Indeed, a post-hoc analysis showed that long-care females switched habitat selection from strong selection when with yearling cubs to a tendency to avoid human habitations when with 2-year-old cubs (Appendix 4.2: Table A4.3 & Figures A4.2-A4.5). Although based on a small sample size, this suggests that some females may decide to remain closer to human habitations temporarily during the mating season, increasing their probability of keeping their yearlings for an additional year. This is in line with a previous study showing that females with cubs-of-the-year alter their habitat selection patterns towards human habitations only during the mating season (Steyaert et al. 2013b). Evaluating intra-individual changes in habitat selection behavior according to female reproductive state and relative fitness outcome would be helpful to infer causality, but this goes beyond the scope of this study.

In a previous study from the same population, we found within-individual consistencies in the duration of maternal care, with two female tactics: short- and long-care females (Van de Walle et al. 2018). The costs and benefits in terms of reproduction and survival are opposed between the two tactics, yielding overall similar fitness output under average hunting pressure. Due to insufficient sample size, we did not test for repeatability of habitat selection behavior here, although it is a reasonable possibility that there are also two distinct female tactics with regard to habitat selection (Leclerc et al. 2016). However, repeatability of maternal care is around 30% (Van de Walle et al. 2018), which also indicates potential for environmentally-driven intra-individual variation in this trait. Such variation may result from undesirable male intervention, or alternatively, from an active female-based decision to prolong maternal care in response to offspring needs or environmental conditions, with sexual segregation during the mating season as one mechanism to achieve this.

Seldom has sexual conflicts over the duration of maternal care been investigated at later stages of maternal care. This gap in knowledge is surprising, considering the large number of species with variable and long periods of mother-offspring association. As it reduces male reproductive opportunities, long mother-offspring association periods are expected to be fertile grounds for sexual conflicts in polygynous species. Males could thus play an important, and potentially under-appreciated, role in the termination of maternal care, resulting in selective pressures on females to adopt tactics to regain power over their allocation decisions. As such, our study provides a new contribution to our limited understanding of the factors determining the duration of maternal care. Previous studies have shown how human activities can affect animal behaviors (Ciuti et al. 2012) and sexual selection (e.g. Allendorf and Hard 2009). We show that females have the potential to take advantage of a human-dominated landscape to reduce their interactions with males and modulate their maternal investment. Our study reinforces the conclusion that human activities may shape sexual selection and offer a new perspective on how sexual conflicts can be mitigated.

4.8 Compliance with ethical standards

Our use of animals followed all applicable national guidelines. Our handling of study animals was approved by the appropriate authorities and ethical committee: the Swedish Board of Agriculture (no. 35-846/03, 31-7885/07, 31-11102/12), the Uppsala Ethical Committee on Animal Experiments (no. C40/3, C47/9, C7/12), and the Swedish Environmental Protection Agency (no. 412-7327-09 Nv).

4.9 Conflict of Interest

The authors declare that they have no conflict of interest.

4.10 Data availability

All data generated or analysed during this study are included as supplementary material.

4.11 Funding

JVdW and ML were financially supported by the Natural Sciences and Engineering Research Council of Canada (NSERC). FP was funded by NSERC discovery grant and by the Canada Research Chair in Evolutionary Demography and Conservation. The Scandinavian Brown Bear Research Project is funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Austrian Science Fund, and the Swedish Association for Hunting and Wildlife Management.

4.12 References

Agrell J, Wolff JO, Ylönen H (1998) Counter-strategies to infanticide in mammals: costs and consequences. Oikos 83:507–517

Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. P Natl Acad Sci USA 106:9987–9994

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Arnemo JM, Evans A, Fahlman Å (2011) Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Hedmark University College, Evenstad, Norway

Arnqvist G, Rowe L (2005) Sexual conflict. Princeton University Press, Princeton, NJ

Balme GA, Hunter LTB (2013) Why leopards commit infanticide. Anim Behav 86:791–799

Balme GA, Robinson HS, Pitman RT, Hunter LTB (2017) Flexibility in the duration of parental care: female leopards prioritise cub survival over reproductive output. J Anim Ecol 86:1224–1234

Bateman AJ (1948) Intra-sexual selection in *Drosophila*. Heredity 2:349–368

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bellemain E, Swenson JE, Taberlet P (2006) Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. Ethology 112:238–246

Ben-David M, Titus K, Beier LR (2004) Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? Oecologia 138:465–474

Bischof R, Bonenfant C, Rivrud IM, Zedrosser A, Friebe A, Coulson T, Mysterud A, Swenson JE (2018) Regulated hunting re-shapes the life history of brown bears. Nat Ecol Evol 2:116–123

Bischof R, Swenson JE, Yoccoz NG, Mysterud A, Giminez O (2009) The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. J Anim Ecol 78:656–665

Boyce MS (1981) Beaver life-history responses to exploitation. J Appl Ecol 18:749–753

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK. (2002) Evaluating resource selection functions. Ecol Model 157:281–300

Bruce HM (1959) An exteroceptive block to pregnancy in the mouse. Nature 184:105

Chapman T, Arnqvist G, Bangham J, Rowe L (2003) Sexual conflict. Trends Ecol Evol 18:41–47

Ciuti S, Northrup JM, Muhly TB, Simi S, Musiani M, Pitt JA, Boyce MS (2012) Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. PLoS ONE 7:e50611

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ

Craighead JJ, Sumner JS, Mitchell JA (1995) The grizzly bears of Yellowstone. Their ecology in the Yellowstone ecosystem. Island Press, Washington DC

Dahle B, Swenson JE (2003a) Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring. Behav Ecol Sociobiol 54:352–358

Dahle B, Swenson JE (2003b) Family break-up in brown bears: are young forced to leave? J Mammal 84:536–540

Dahle B, Swenson JE (2003c) Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. J Anim Ecol 72:660–667

Elfström M, Davey ML, Zedrosser A, Müller M, De Barba M, Støen O-G, Miquel C, Taberlet P, Hackländer K, Swenson JE (2014a) Do Scandinavian brown bears approach settlements to obtain high-quality food? Biol Conserv 178:128–135

Elfström M, Zedrosser A, Jerina K, Støen O-G, Kindberg J, Budic L, Jonozovič M, Swenson JE (2014b) Does despotic behavior or food search explain the occurrence of problem brown bears in Europe? J Wildlife Manage 78:881–893

Elliot NB, Valeix M, Macdonald DW, Loveridge AJ (2014) Social relationships affect dispersal timing revealing a delayed infanticide in African lions. Oikos 123:1049–1056

Fairbanks LA, McGuire MT (1987) Mother-infant relationships in vervet monkeys: response to new adult males. Int J Primatol 8:351–366

Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor 19:16–36

Gosselin J, Leclerc M, Zedrosser A, et al (2017) Hunting promotes sexual conflict in brown bears. J Anim Ecol 86:35–42

Grüebler MU, Naef-Daenzer B (2008) Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. Ecology 89:2736–2745

Hertel AG, Leclerc M, Warren D, Pelletier F, Zedrosser A, Mueller T (2019) Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. Anim Behav 147:91–104

Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol 1:13–40

Johnson CJ, Nielsen SE, Merrill EH, McDonald TL, Boyce MS (2006) Resource selection functions based on use – availability data: theoretical motivation and evaluation methods. J Wildlife Manage 70:347–357

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Leclerc M, Vander Wal E, Zedrosser A, Swenson JE, Kindberg J, Pelletier F (2016) Quantifying consistent individual differences in habitat selection. Oecologia 180:697–705

Lee PC, Majluf P, Gordon IJ (1991) Growth, weaning and maternal investment from a comparative perspective. J Zool 225:99–114

Lele SR, Merrill EH, Keim J, Boyce MS (2013) Selection, use, choice and occupancy: clarifying concepts in resource selection studies. J Anim Ecol 82:1183–1191

Lessels CM (1999) Sexual conflict in animals. In: Keller L (ed) Levels of selection in evolution. Princeton University Press, Princeton, NJ, pp 75–99

Lessels CM (2012) Sexual conflict. In: Royle NJ, Smiseth PT, Kölliker M (eds) The evolution of parental care. Oxford University Press, Oxford, pp 150–170

Lewis JS, Rachlow JL, Garton EO, Vierling LA (2007) Effects of habitat on GPS collar performance: using data screening to reduce location error. J Appl Ecol 44:663–671

Libal NS, Belant JL, Leopold BD, Wang G, Owen PA (2011) Despotism and risk of infanticide influence grizzly bear den-site selection. PLoS ONE 6:e24133

Loseto LL, Richard P, Stern GA, Orr J, Ferguson SH (2006) Segregation of Beaufort Sea beluga whales during the open-water season. Can J Zool 84:1743–1751

Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biol Conserv 134:548–558

Lukas D, Huchard E (2014) The evolution of infanticide by males in mammalian societies. Science 346:841–844

Main MB, Weckerly FW, Bleich VC (1996) Sexual segregation in ungulates: new directions for research. J Mammal 77:449–461

Martin AR, da Silva VMF (2004) River dolphins and flooded forest: seasonal habitat use and sexual segregation of botos (*Inia geoffrensis*) in an extreme cetacean environment. J Zool 263:295–305

Martin P (1984) The meaning of weaning. Anim Behav 32:1257–1259

Matson G, Van Daele L, Goodwin E, Aumiller L, Reynolds H, Hristienko H (1993) A laboratory manual for cementum age determination of Alaska bear first premolar teeth. Matson's Laboratory, Milltown

McLellan (1994) Density-dependent population regulation in brown bears. In: Taylor M (ed) Density dependent population regulation of black, brown and polar bears. The ninth international conference on bear research and management. International Association for Bear Research and Management, Missoula, MT, USA

Mohr CO (1947) Table of equivalent populations of North American small mammals. Am Midl Nat 37:223–249

Morino L, Borries C (2017) Offspring loss after male change in wild siamangs: the importance of abrupt weaning and male care. Am J Phys Anthropol 162:180–185

Oksanen J, Blanchet G, Friendly M et al (2017) vegan: community ecology package. R package version 2.4-2, https://cran.r-project.org/web/packages/vegan/index.html

Ordiz A, Støen O-G, Sæbø S, Kindberg J, Delibes M, Swenson JE (2012) Do bears know they are being hunted? Biol Conserv 152:21–28

Rode KD, Farley SD, Robbins CT (2006) Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. Ecology 87:2636–2646

Sandell MI, Smith HG (1996) Already mated females constrain male mating success in the European starling. Proc R Soc Lond B 263:743–747

Shuster SM, Wade MJ (2003) Mating systems and strategies. Princetown University Press, Princeton, NJ

Skuban M, Find'o S, Kajba M (2018) Bears napping nearby: daybed selection by brown bears (*Ursus arctos*) in a human-dominated landscape. Can J Zool 96:1–11

Smultea MA (1994) Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. Can J Zool 72:805–811

Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. Adv Stud Behav 22:1–63

Solberg KH, Bellemain E, Drageset O-M, Taberlet P, Swenson JE (2006) An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. Biol Conserv 128:158–168

Spady TJ, Lindburg DG, Durrant BS (2007) Evolution of reproductive seasonality in bears. Mamm Rev 37:21–53

Steyaert SMJG, Endrestøl A, Hackländer K, Swenson JE, Zedrosser A (2012) The mating system of the brown bear *Ursus arctos*. Mamm Rev 42:12–34

Steyaert SMJG, Kindberg J, Swenson JE, Zedrosser A (2013a) Male reproductive strategy explains spatiotemporal segregation in brown bears. J Anim Ecol 82:836–845

Steyaert SMJG, Leclerc M, Pelletier F, Kindberg J, Brunberg S, Swenson JE, Zedrosser A (2016) Human shields mediate sexual conflict in a top predator. Proc R Soc B 283:20160906

Steyaert SMJG, Reusch C, Brunberg S, Hackländer K, Zedrosser A (2013b) Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. Biol Lett 9:20130624

Steyaert SMJG, Swenson JE, Zedrosser A (2014) Litter loss triggers estrus in a nonsocial seasonal breeder. Ecol Evol 4:1–11

Støen O-G, Ordiz A, Evans AL, Laske TG, Kindberg J, Fröbert O, Swenson JE, Arnemo JM (2015) Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). Physiol Behav 152:244–248

Suring LH, Farley SD, Hilderbrand GV, Goldstein MI, Howlin S, Erickson WP (2007) Patterns of landscape use by female brown bears on the Kenai Peninsula, Alaska. J Wildlife Manage 70:1580–1587

Swenson JE, Adamič M, Huber D, Stokke S (2007) Brown bear body mass and growth in northern and southern Europe. Oecologia 153:37–47

Swenson JE, Dahle B, Sandegren F (2001) Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. Ursus 12:81–92

Tarwater CE, Brawn JD (2010) The post-fledging period in a tropical bird: patterns of parental care and survival. J Avian Biol 41:479–487

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man. Aldine Publishing Company, Chicago, IL

Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249–264

Van de Walle J, Pigeon G, Zedrosser A, Swenson JE, Pelletier F (2018) Hunting regulation favors slow life histories in a large carnivore. Nat Commun 9:1100

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat 100:687–690

Zedrosser A, Pelletier F, Bischof R, Festa-Bianchet M, Swenson JE (2013) Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations. Ecology 94:231–240

Zhao Q, Borries C, Pan W (2011) Male takeover, infanticide, and female countertactics in white-headed leaf monkeys (*Trachypithecus leucocephalus*). Behav Ecol Sociobiol 65:1535–1547

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

CHAPITRE 5
POTENTIEL SÉLECTIF DE LA CHASSE SUR LA DURÉE DES SOINS MATERNELS

5.1 Description de l'article et contribution

Chez l'ours brun scandinave, les observations issues du suivi à long-terme de la population montrent qu'au cours des 20 dernières années, les femelles prodiguent des soins maternels plus longs. On suspectait alors que la réglementation de la chasse interdisant de tuer des membres de groupes familiaux (c.-à-d. des femelles reproductrices et leurs jeunes dépendants), couplée à une forte pression de chasse (~30 %), pourrait artificiellement favoriser les femelles prodiguant des soins maternels longs et sélectionner pour une plus longue durée de soins maternels dans la population. Cet article visait à confirmer le potentiel sélectif de la protection légale des groupes familiaux et à aborder les conséquences possibles d'un changement en durée de soins maternels induit par l'Homme sur les processus démographiques chez l'ours brun scandinave.

Je me suis inspirée des réflexions d'Andreas Zedrosser, Fanie Pelletier et Jon E Swenson pour élaborer l'idée initiale pour cet article. Ensuite, j'ai développé cette idée en collaboration avec Fanie Pelletier, Andreas Zedrosser et Jon E. Swenson. J'ai réalisé les analyses et écrit la première version du manuscrit. Gabriel Pigeon a contribué aux analyses en fournissant des suggestions et en développant la méthode d'évaluation de l'effet de la chasse sur la valeur adaptative des deux tactiques de soins maternels. Tous les auteurs ont participé à l'interprétation des résultats et aux révisions du manuscrit. Andreas Zedrosser et Jon E. Swenson ont coordonné les activités du SBBRP. DOI: 10.1038/s41467-018-03506-3.

Hunting regulation favors slow life histories in a large carnivore

Nature Communications (2018), 9:1100

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https://doi.org/10.1038/s41467-018-03506-3

5.2 Abstract

As an important extrinsic source of mortality, harvest should select for fast reproduction and accelerated life histories. However, if vulnerability to harvest depends upon female reproductive status, patterns of selectivity could diverge and favor alternative reproductive behaviors. Here, using more than 20 years of detailed data on survival and reproduction in a hunted large carnivore population, we show that protecting females with dependent young, a widespread hunting regulation, provides a survival benefit to females providing longer maternal care. This survival gain compensates for the females' reduced reproductive output, especially at high hunting pressure, where the fitness benefit of prolonged periods of maternal care outweighs that of shorter maternal care. Our study shows that hunting regulation can indirectly promote slower life histories by modulating the fitness benefit of maternal care tactics. We provide empirical evidence that harvest regulation can induce artificial selection on female life history traits and affect demographic processes.

5.3 Introduction

The strong potential for human harvest to alter ecological and evolutionary processes has been recognized in marine systems, where harvest pressure has direct and indirect effects on both fish yield and economic revenue[1–4]. Size-selective harvest of larger fish favors maturation at smaller sizes and reduces yield[5]. In terrestrial systems, trophy hunting can artificially increase mortality of individuals with large horns, tusks, or antlers, which can induce selective pressures and lead to evolutionary changes in heritable morphological traits that cannot be quickly reversed by natural selection[6–8]. Although it is easily conceivable that size-selective harvest regimes can alter patterns of natural selection and cause demographic changes in wildlife populations, such effects are usually less expected and thereby less studied in harvest regimes that are not size selective[9]. However, theoretical models show that size-independent harvest can also induce selective pressures on life history traits[10–13], and recent empirical work has documented harvest selectivity for age, sex, and behavioral traits in the wild[14–16]. Despite its importance for management, we still know very little about the consequences of such selectivity on population processes.

Fitness is maximized by allocating resources to survival or reproduction and the function over which allocation will be biased depends on levels of extrinsic mortality[17]. Under high extrinsic mortality, fitness can be optimized by higher investment in reproduction, leading to selection for faster life histories[5,13], similar to what would be expected under natural selection. This acceleration in the pace of life has been documented in several harvested populations, which suggests that harvest should lead to r-selection[2,13,16,18]. Moreover, even in the absence of any harvest preferences, individuals can differ in vulnerability to harvest, depending on behavior, harvest methods, and regulations[16,19–21]. Indeed, in several sport hunting systems, the killing of females with dependent offspring is either illegal, discouraged, or avoided by hunters to protect the female segment of the population or because of the potentially lowered survival of orphaned offspring that can cause ethical, as

well as demographic, issues[22–25]. In such systems, reproducing females are less vulnerable to hunting and thus should enjoy an artificial selective advantage that is accentuated with increasing hunting pressure. This type of harvest selectivity could promote longer periods of mother-offspring associations and slower life histories, with potential consequences for population dynamics. Although the potential selective and demographic effects of the protection of females based on reproductive status have already been acknowledged[20,22–27], these effects have rarely been quantitatively assessed using empirical data[16].

Here, we test whether a hunting regulation that prohibits the killing of females with dependent offspring can induce selectivity on female reproductive tactics at the individual level and evaluate the effect of such selectivity on population processes. We use more than 20 years of exceptionally detailed individual-based data on survival and reproduction in a heavily hunted population of brown bears (*Ursus arctos*) in Sweden[28], where two distinct maternal care tactics have been documented[29]. We start by documenting the temporal trend in the duration of maternal care and contrasting survival probabilities between females providing either short (1.5-year tactic) or long (2.5-year tactic) maternal care. Longer maternal care entails a loss of reproductive opportunities in species where breeding is not resumed until current offspring are weaned[30]. Therefore, we compare two demographically and evolutionary meaningful proxies of fitness[31] that integrate information on survival and reproduction, i.e., asymptotic population growth rate (λ; the annual per capita rate of population increase[32]) and net reproductive rate, R_0 (number of females an individual is expected to produce over its lifetime[31,33]), between the two maternal care tactics to quantify the difference in fitness between these tactics. Finally, we complement this analysis by evaluating the fitness pay-off of each maternal care tactic under various plausible scenarios of hunting pressure to determine if hunting can drive the relative occurrence of maternal care tactics in the population.

We show that being in a family group and providing longer maternal care results in a survival advantage for both adult females and dependent offspring. This survival advantage compensates for a reduction in reproductive output for females providing longer maternal care. As a result, both maternal care tactics have similar fitness values on average, but as hunting pressure increases, longer maternal care yields higher fitness returns. Protecting females with dependent young has therefore the potential to induce selectivity towards a lengthening of maternal care in the Scandinavian brown bear, with consequences for population generation time and age structure.

5.4 Results

5.4.1 Occurrence of maternal care tactics in the population

We found that from 1987 to 2015, the odds of a litter being weaned after 2.5 years of maternal care increased by a factor 1.17 (95% CI = [1.07, 1.29]) annually in the population (n = 164 litters from 62 individual females). The first documented litter in our study population that was raised with the 2.5-year tactic was born in 1993 and weaned in 1995, and since then 24.8% of the litters have received 2.5 years of maternal care; the rest received maternal care for 1.5 years (Figure 5.1).

5.4.2 Protective effect of maternal care

Adult (≥ 4 years-old (y.o.)) and yearling female brown bears in a family group during the hunting season have a survival advantage compared to when solitary (Figure 5.2a). For adult females, being solitary during the hunting season significantly reduces survival

probability (oddsratio: 0.30, 95% CI = [0.16, 0.57]). The annual finite mortality rate of solitary adult females was 0.16 (95% CI = [0.12, 0.20], n = 407 bear-years) and the hunting-induced annual finite mortality rate was 0.14 (95% CI = [0.10, 0.17], 55 cases). In contrast, the annual finite mortality rate of adult females accompanied by dependent offspring (i.e. member of a family group) was only 0.06 (95% CI = [0.03, 0.10], n = 207 bear-years, Figure 5.2b) and the hunting-induced annual finite mortality rate was 0.04 (95% CI = [0.02, 0.07], 9 cases during the study period 1993-2015, where a hunter accidentally shot the female before observing the dependent offspring). Therefore, the odds of dying from hunting were 3.91 times higher for solitary females compared to adult females accompanied by dependent offspring.

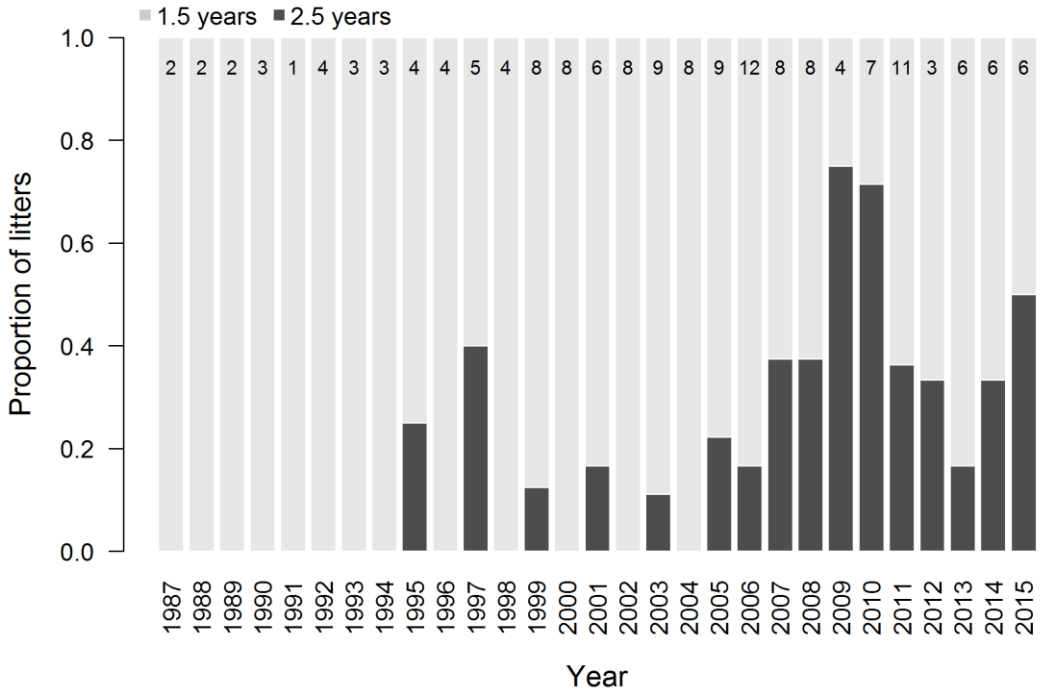

Figure 5.1 Proportion of successfully weaned brown bear litters that had received 1.5 years and 2.5 years of maternal care in south-central Sweden from 1987-2015.

Sample size for each year is indicated on top of each bar.

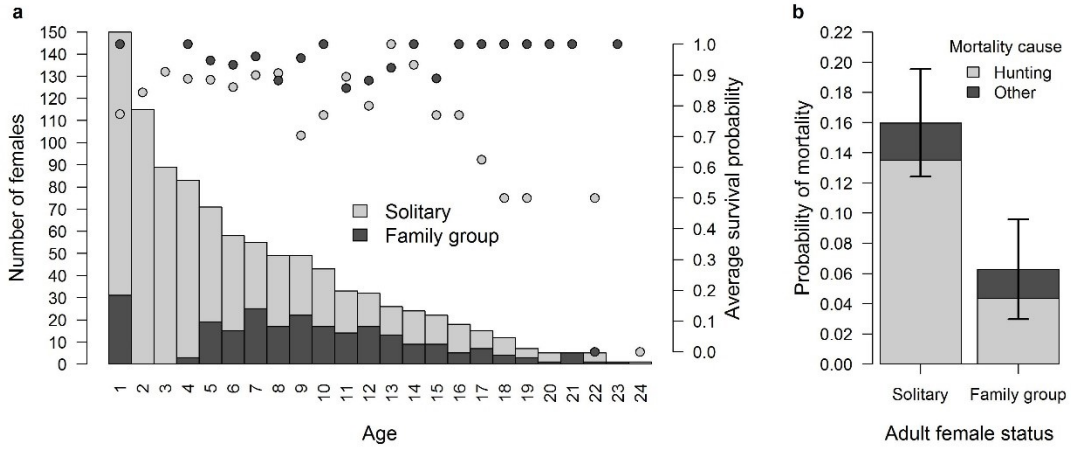

Figure 5.2 Protective effect of being in a family group for female brown bears in south-central Sweden from 1993-2015.

a, Age-specific number (bars, left axis) and average survival probability (dots, right axis) of female brown bears according to their status (solitary: light gray; member of a family group: dark gray). All cubs-of-the-year (age = 0) are dependent upon their mother and are protected from hunting by regulation, however, they are not represented in this figure, because their sex could not be determined. **b**, Adult female probability of mortality (average and 95% CI) from hunting and other causes according to their reproductive status (solitary, n=407; member of a family group, n=207).

5.4.3 Tactic-based demographic analyses

Focusing from 1993 to 2015, when both maternal care tactics coexisted in the population, we found that individual females had consistent durations of maternal care (repeatability = 0.33, 95% CI = [0.11, 0.47]), suggesting that the population includes two distinct behavioral tactics regarding maternal care. Most females (62.5%) consistently provided maternal care for 1.5 or 2.5 years exclusively, whereas the rest could alternate between the

1.5-year and 2.5-year tactics, but using one of the two tactics more frequently. Females that we considered to be consistent in their maternal care tactic were not older on average (mean = 10.88 y.o., 95% CI = [9.65, 12.11], n = 25) than more flexible females (mean = 12.07 y.o., 95% CI = [10.34, 13.81]; t_{38} = -1.12, P = 0.27, n = 15). Primiparous females had a similar probability of using the 1.5-year tactic compared to multiparous females (odds-ratio = 0.46, 95% CI = [0.05, 4.67], n = 123), suggesting that maternal experience was not the main factor explaining differences in maternal care tactics. Therefore, we separated adult females according to the duration of maternal care they provided and young females (≤ 3 y. o.) according to the duration of maternal care they had received as cubs. We estimated tactic- and age-specific demographic rates (Appendix 5.1: Table A5.1), survival, and recruitment as the number of yearling daughters produced per year per female, following the previously described age structure (Appendix 5.1: Figure A5.1) in this population34. We found that age class and maternal care tactic were both important factors explaining variation in survival (Table 5.1). Prime-age females, aged 4-8 y.o., enjoyed the highest survival independently of maternal care tactic. Overall, the odds of surviving were 2.14 higher (95% CI = [1.21, 3.79]) for females using the 2.5-year tactic and the difference in predicted survival probabilities, all age classes combined, was 5.1% between the two maternal care tactics (average predicted survival probability for the 2.5-year tactic: 0.95, average predicted survival probability for the 1.5-year tactic: 0.90). This clearly shows the survival benefit of longer periods of maternal care for both young and adult females. The interaction between tactic and age class did not improve model fit significantly (Table 5.1), suggesting that the management regulation has a protective effect for all age classes. Increased survival probability for the 2.5-year tactic, however, was most apparent in yearling and adult females (Figure 5.3), because only those age classes benefit from the protective regulation. In comparison, survival probabilities were similar between maternal care tactics for 2- and 3-year-olds, because at those ages all females are independent from their mothers and are thus equally vulnerable to hunting. Survival analyses produced another key result; all female yearlings raised with the 2.5-year tactic survived when accompanying their mother in their second year, whereas independent yearling females had a lower survival probability of 0.78 ± 0.04 (Appendix 5.1: Table A5.1). However, since

adult females cannot mate prior to weaning their offspring, they will have fewer reproductive opportunities when using the 2.5-year tactic. Indeed, we found that using the 2.5-year maternal care tactic reduces adult females recruitment (Table 5.1), which was 34.6% lower (yearly recruitment = 0.25) compared to the 1.5-year tactic (yearly recruitment = 0.38; Table 5.2).

Table 5.1 Parameter estimates from final statistical models comparing tactic- and age class-specific demographic rates for female brown bears in south-central Sweden from 1993-2015

	Coefficient	95% CI Lower	95% CI Upper	z-value	P-value
Survival					
Intercept	1.430	1.015	1.887	6.489	< 0.0001
2.5-year tactic	0.761	0.214	1.365	2.610	0.009
Age class 2 y.o†.	0.238	-0.434	0.934	0.685	0.494
Age class 3 y.o.	0.932	0.099	1.887	2.071	0.038
Age class 4-8 y.o.	2.124	1.219	3.230	4.229	< 0.0001
Age class 9+ y.o.	0.224	-0.335	0.769	0.798	0.425
	Variables removed§ :				
	*Tactic*Age class (X^2 = 7.920, P = 0.095)*				
Recruitment					
Intercept	-0.923	-1.154	-0.697	-7.924	< 0.0001
2.5-year tactic	-0.425	-0.860	-0.003	-1.948	0.051
	Variables removed :				
	*Tactic*Age class (X^2 = 1.935, P = 0.164)*				
	Age class (X^2 = 0.969, P = 0.325)				

Parameters come from binomial and negative binomial models of survival probability and recruitment rate (i.e. the number of yearling daughters produced per female per year), respectively. Variables were removed if their inclusion did not improve model fit according to likelihood ratio tests. Results are presented on their transformed scale to show statistical significance.† y.o. = years-old. §* is used to represent interactions.

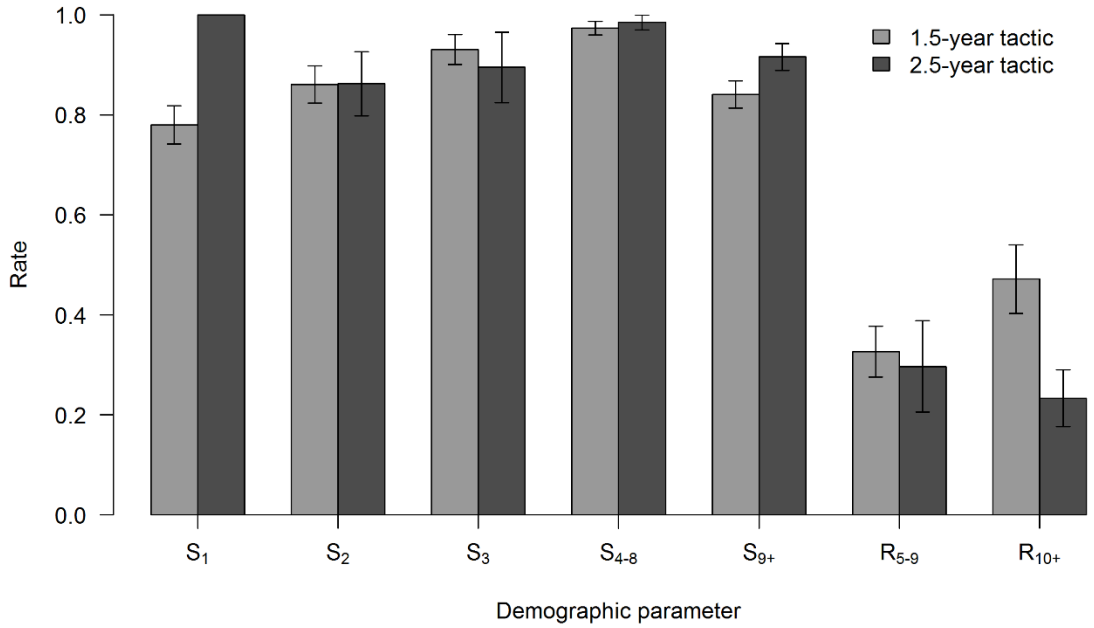

Figure 5.3 Empirical values of tactic- and age class-specific demographic rates for female brown bears in south-central Sweden from 1993-2015.

Bars represent 95% confidence intervals. Definitions: S = annual finite survival rate and R = recruitment, i.e., the number of yearling daughters produced per female per year, S_1 = survival of yearlings, S_2 = survival of 2 year-olds (y.o.), S_3 = survival of 3 y.o., S_{4-8} = survival of 4-8 y.o., S_{9+} = survival of 9 y.o. and older, R_{5-9} = recruitment of 5-9 y.o., and R_{10+} = recruitment of 10 y.o. and older. The descriptive statistics presented on the figure and sample sizes can be found in Supplementary Table 1.

The two maternal care tactics have contrasting costs and benefits for survival and reproduction, the two main components of individual fitness. That raises a crucial question: which tactic yields the highest overall fitness? Incorporating model predictions for tactic- and age-specific survival probabilities and recruitment (Table 5.2) into tactic-based population matrices yielded an asymptotic population growth rate (λ) of 1.09 (95% CI = [1.05, 1.14]) for the 1.5-year tactic, and of 1.10 (95% CI = [1.05, 1.15]) for the 2.5-year tactic. The net reproductive rate tended to be lower for the 1.5-year tactic, 2.26 (95% CI = [1.54, 3.22] compared to the 2.5-year tactic, 3.32 (95% CI = [1.68, 6.23]). However, both tactics yielded overlapping confidence intervals and bootstrapped distributions of λ and R_0 (Figure 5.4a,b), suggesting similar fitness over the study period.

Although λ and R_0 were similar between maternal care tactics, other population processes may be affected by a switch in maternal care tactics in the population. First, generation time, T, (i.e., the time required for the population to be multiplied by its net reproductive rate, R_0[33]) would be lengthened by about 3 years, should the population be comprised of only females using the 2.5-year tactic (mean generation time 1.5-year tactic: 8.95 years, 95% CI = [8.08, 10.27]; mean generation time 2.5-year tactic: 12.05 years (95% CI = [10.03, 15.24]). Although the bootstrapped distributions of generation times slightly overlapped (Figure 5.4c), the simulated generation times for the 2.5-year tactic had a 99.5% probability of being higher than for the 1.5-year tactic. A hunting regulation favoring the 2.5-year tactic is thus most likely to promote slower life histories in this population. Second, stable age structures extracted from the tactic-specific matrix models contained more adult females within the 2.5-year tactic compared to the 1.5-year tactic (64.8% vs. 57.2%; Figure 5.4d).

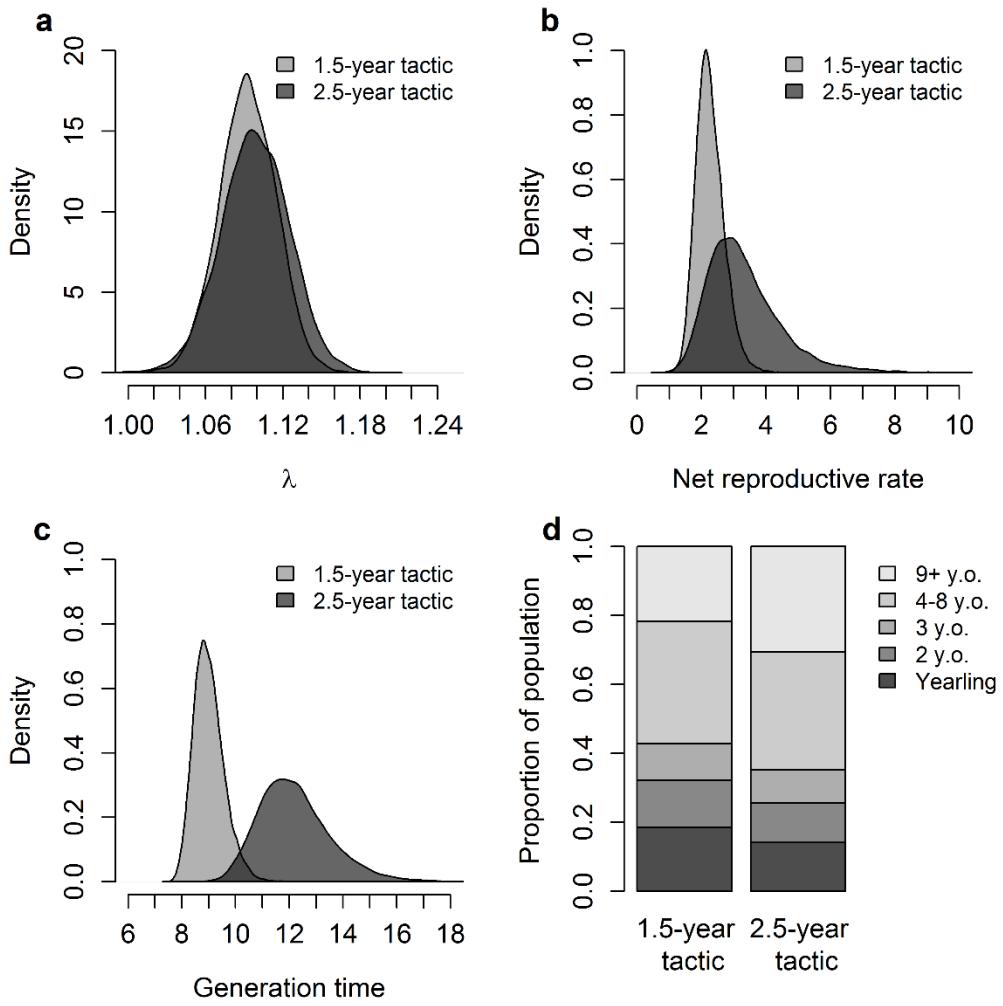

Figure 5.4 **Contrasted demographic parameters of the two brown bear maternal care tactics in south-central Sweden, 1993-2015.**

Asymptotic population growth rates, λ, (**a**), net reproductive rates, R_0, (**b**), generation times, T, (**c**) and stable age structures (**d**) were extracted from tactic-based population matrices using bootstrapped predictions of age class-specific survival probabilities and recruitment (10,000 predictions per demographic parameter per age class, yielding 10,000 different population matrices). Table 2 shows the bootstrapped model predictions for age-specific survival probabilities and recruitment rates that were used in the population matrices to generate the demographic parameters for each tactic.

Table 5.2 **Bootstrapped model-based predictions (back-transformed on the original scale) of tactic- and age class-specific demographic rates for female brown bears in south-central Sweden, 1993-2015**

	1.5-year tactic			2.5-year tactic		
		95% CI			95% CI	
	Mean estimate	Lower	Upper	Mean estimate	Lower	Upper
Survival						
S_1	0.809	0.739	0.874	0.903	0.833	0.951
S_2	0.844	0.767	0.911	0.922	0.860	0.966
S_3	0.916	0.851	0.974	0.961	0.914	0.988
$S_{4\text{-}8}$	0.973	0.947	0.994	0.988	0.971	0.997
S_{9+}	0.841	0.789	0.889	0.920	0.874	0.957
Recruitment						
$R_{5\text{-}9}$*	0.384	0.296	0.482	0.251	0.167	0.351
R_{10+} †	0.384	0.296	0.482	0.251	0.167	0.351

Model predictions were bootstrapped 10,000 times to generate average estimates and 95% confidence intervals. Definitions: S = survival and R = recruitment, i.e., the number of yearling daughters produced per female per year, S_1 = survival of yearlings, S_2 = survival of 2 year-olds (y.o.), S_3 = survival of 3 y.o., $S_{4\text{-}8}$ = survival of 4-8 y.o., S_{9+} = survival of 9 y.o. and older, $R_{5\text{-}9}$ = recruitment of 5-9 y.o., and R_{10+} = recruitment of 10 y.o. and older. * Because reproductive rates are represented by fecundities ($Fecundity_t = Survival_{(t\rightarrow t+1)} \times Recruitment_{t+1}$) in the tactic-specific matrix models, recruitment was estimated for age classes 5-9 and 10+ years to follow age classes for survival, and because 5 years is the youngest age at which females may start producing yearlings in our study population.

†Age class did not significantly affect recruitment rate, thus, age class 5-9 and 10+ years were assigned a similar recruitment value in matrix models.

5.4.4 Differential effects of hunting between tactics

We found that the fitness benefit of prolonged maternal care increases with increasing levels of hunting pressure. Over the study period, hunting pressure varied from 0% to 34% (Appendix 5.1: Figure A5.2). By allowing survival components to vary as a function of observed hunting pressure in the tactic-specific population matrices, we show that, whereas λ decreases steadily with increasing hunting pressure for the 1.5-year tactic, it remains relatively unaffected by hunting pressure for the 2.5-year tactic (Figure 5.5). This suggests that hunting may affect the relative occurrence of reproductive tactics in populations subject to a hunting regime that is selective regarding female reproductive status.

5.5 Discussion

Humans as predators are a dominant agent of mortality in wildlife populations[1] imposing a selective landscape that vary both in its strength and phenotypic targets[14,15,18,20,35]. Here, we show that a hunting regulation based on female reproductive status can improve the survival prospects of female brown bears that provide longer maternal care, thereby promoting slow life histories, with consequences for population processes.

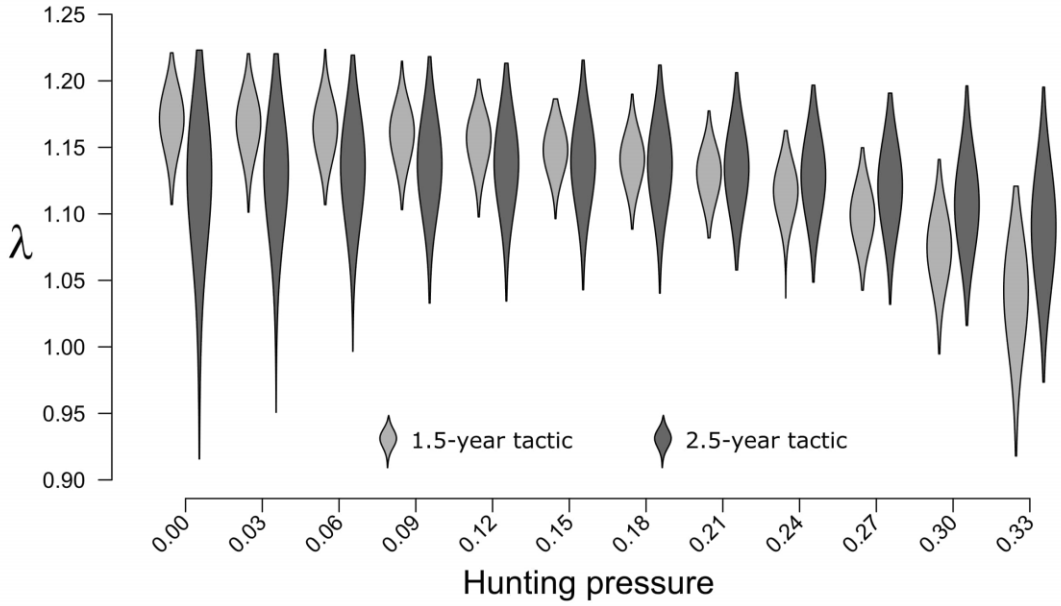

Figure 5.5 Differential effect of hunting pressure on the fitness of brown bear maternal care tactics in south-central Sweden, 1993-2015.

Predicted effect of hunting pressure (number of marked bears that were shot in a given year divided by the number of marked bears available for hunting that same year) on the asymptotic population growth rate, λ, for each maternal care tactic. The violins represent the density plots of lambda (1,000 iterations) at each hunting pressure simulated. Estimates of the effect of hunting pressure on tactic- and age class-specific survival probabilities are given in Supplementary Table 5.2.

Over the study period, both maternal care tactics yielded overlapping asymptotic population growth. This might appear surprising, considering that differences in recruitment (35.2%) are larger than differences in survival probability (5.1%) between the two tactics. However, because the elasticities of demographic rates in long-lived mammals are usually larger for survival than for reproduction[34,36,37], the gain in survival for females

using the 2.5-year tactic may explain the similar fitness between the two tactics. The artificial gain in survival through prolonged maternal care due to legal protection from hunting can compensate for reduced reproductive output in hunting systems where family groups are protected. In a Swedish population of moose (*Alces alces*), where calves must be shot first before hunters are allowed to kill the mother, regulations artificially reduce the costs of reproduction by lowering the mortality of females with dependent calves, because calves act as a shield or because hunters prefer to harvest nonlactating females[26]. Moreover, because it integrates the survival probabilities of both adults and offspring, the lack of differences in λ between the two tactics may also be explained partially by differences in offspring survival. Indeed, longer maternal care may increase offspring survival probabilities through higher energy intake and additional protection from other causes of mortality that independent offspring may face. In leopards (*Panthera pardus*), longer maternal care in adverse years acts as a buffer against prey scarcity, which compensates a female's loss of reproductive opportunities[30]. Here, we show that the survival gain due to management regulations can compensate for reduced recruitment, but also promote alternative maternal care tactics in harvested populations.

Over the study period, we expected that shorter periods of maternal care would be more advantageous, because it provides females with more reproductive opportunities and because the energetic costs associated with maternal care are high in mammals[38]. Also, strong historical persecution, regardless of reproductive status, has favored high investment in reproduction in the Scandinavian brown bear[39]. The resulting short interbirth intervals have been a key element for the rapid recovery of the population, that increased from about 130 individuals in the 1930s to around 2800 in 2013, following the implementation of protective measures[40]. Rapid reproduction is especially advantageous in expanding populations below carrying capacity, but as population density increases investment into survival becomes more advantageous[41]. Compared to its historic value, our study population is currently experiencing a reduction in its growth rate[34,40], which could explain why fast reproduction may be less advantageous today, even with relatively lower levels of

hunting pressure. In addition, it is possible that intraspecific killing of yearlings, an important cause of mortality for female yearlings[42], may be higher today. Indeed, because surviving male bears reorganize their homes ranges after the death of a nearby male[43], hunting can promote spatial reorganization, which, combined with higher numbers of bears in the population in general, leads to higher probabilities of deadly encounters between young bears and adult males[42,44]. By staying with their mother an additional year, yearlings not only gain protection against hunting, but also against their other main cause of mortality; intraspecific killing[28,42]. The survival benefit of prolonged maternal care did not carry over, however, as the survival probabilities were similar between tactics for age classes 2 and 3 y.o, which is in line with other studies in birds and mammals that have found contradicting results from carry over effects of the duration of maternal care[30,45]. However, in the context where maternal care acts as a shield against hunting, prolonged maternal care has the additional advantage of reducing the period of vulnerability between weaning/independence and first reproduction, when further protection from hunting can be obtained.

The relative occurrence of the 2.5-year maternal care tactic has increased in south-central Sweden since 1987. Before 1995, the 2.5-year tactic was unobserved, although this could be due to the lower number of litters monitored in the early stages of the study. Up until 2005, when a larger number of litters has been monitored (n = 84), the 2.5-year tactic remained relatively rare and accounted for only 7.1% of the litters weaned, whereas this percentage increased to 36.3% from 2005 to 2015 (n = 80). Offspring mass and resource availability are often cited as the most important drivers of the duration of maternal care, with smaller offspring usually being cared for longer[29,46]. It is possible that a potential reduction in resources availability could have forced females to extend their maternal care in recent years. However, the abundance of bilberry (*Vaccinium myrtillus*), the most important food resource driving variations in body mass and reproductive success of Scandinavian brown bear females, has shown variations over the last ten years in the study area, but it did not decline[47]. Also, these bears can switch to alternative food items, such as

crowberry (*Empetrum* spp.), when bilberry abundance is low, which suggests that they are less vulnerable to food shortage[48]. Alternatively, an increase in hunting quotas[40] and hunting pressure since 1993 (Appendix 5.1: Figure A5.2) may have disproportionally removed fast-reproducing females, thereby artificially selecting for females that provide longer periods of maternal care in the population. Indeed, we show that the fitness pay-off of each reproductive tactic depends on harvest intensity, with lower hunting pressure selecting for shorter maternal care and higher hunting pressure selecting for longer maternal care. In the side-blotched lizard (*Uta stansburiana*), natural selection favors alternative female reproductive strategies when population density cycles, with slower life histories being selected at high densities[41]. In our study population, although changes in hunting pressure could correlate with density effects, we did not observe a similar trend between the fitness of tactics as a function of population density (Appendix 5.1: Figure A5.3). A more likely explanation for the increasing gap in λ between the tactics with increasing hunting pressure is the overall stronger negative effect of hunting on the survival of females using the 1.5-year tactic, especially of adults and yearlings, compared to females using the 2.5-year tactic (Appendix 5.1: Figure A5.2). Prolonged maternal care provides a buffer against high hunting pressure, as it protects adult females, which are the most productive segment of the population[37], as well as yearlings, which are the most vulnerable individuals[28]. This implies that the relative frequency of female reproductive tactics may alternate over time in the population depending on the level of human exploitation, as previously suggested by a mathematical modeling based on red deer (*Cervus elaphus*) life histories[11]. Over our 22-year study period and under intermediate values of hunting pressure, both tactics showed similar fitness, which suggests that the two phenotypes will likely be maintained in the population, as it is the case in many other brown bear populations[49,50]. However, if levels of hunting pressure continue to be high or increase, our study suggests that the relative occurrence of the 2.5-year tactic will increase.

Despite a similar asymptotic population growth between the 1.5-year and the 2.5-year tactics, a change in maternal care tactic can affect other population processes. Using

simulations, it has been shown in the alpine chamois (*Rupicapra rupicapra*) that selective harvest of nonlactating females may affect age-specific mortality and population age structure, especially at high harvest rates[25]. Here, using empirical data on tactic-specific demographic rates, we show that two hypothetical brown bear populations, one consisting of females using the 1.5-year tactic and the other consisting of females using the 2.5-year tactic, would show different age structures, but without detectable consequences for population growth. This suggests that interactions between hunting pressure and female reproductive tactics likely affect population processes indirectly through other demographically important variables. A shift in population age structure could affect sensitivities of demographic rates and patterns of evolutionary dynamics, which would be missed by focusing on population growth alone[51]. For example, a shift in population age structure towards the adult female segment of the population may further divert the hunt towards solitary adult females and select for even longer maternal care. Moreover, because adult female survival has the greatest elasticities, such a population would be highly sensitive to a removal of the legal protection of family groups. Also, in such a population, harvest-induced evolutionary changes would take even longer to reverse, as generation time would be lengthened.

In this study, we used detailed empirical data from individual-based survival and reproduction to show that a hunting regime protecting females based on their reproductive status can induce selective pressures on female life history traits. The protection of (or unwillingness to kill) females with young is widespread among hunting systems, with examples from a vast range of game species[20,24,25,52,53]. Because of the survival advantage gained by females accompanied by dependent young, there is a great potential to observe selectivity based on female reproductive status in several other hunting systems. This selectivity could be towards longer periods of maternal care in populations where this trait varies[30,46,54–56], or may favor higher investment in reproduction early and late in life. This management-induced selectivity should not be overlooked, as it acts on female life history traits, which are by definition the very drivers of female fitness and population dynamics.

Interestingly, however, a switch in female maternal care tactic had no effect on population growth in our system. Studies investigating indirect effects of hunting by monitoring changes in population growth alone are thus likely to miss important changes in female life histories and demography. Such changes may also impact hunters through a reduction in the availability of adult females and an unintentional, as well as potentially undesirable, hunting bias towards subadult females and males. Understanding how hunting and management regulations interact with animal life histories to affect population processes is thus of great ecological, management, and conservation importance.

5.6 Methods

5.6.1 Study area, bear population, and hunting

The study area is located in Dalarna and Gävleborg counties, south-central Sweden (approximately 61° N, 15° E). The area encompasses 13,000 km^2 of rolling landscape dominated by heavily managed Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) forests. Hunting is the most important source of mortality for adult Scandinavian brown bears[28]. Bears are hunted throughout the study area; the bear hunting season starts in late August and lasts until mid-October or until the regional quota has been filled. No specific license is required to hunt bears in Sweden. Hunting is allowed for anyone possessing hunting rights in a hunting area and a weapon legal for big game hunting[57]. Hunters can kill any solitary bear; however, bears in family groups are protected by law. All successful brown bear hunters must notify an officially appointed inspector on the day of the kill.

Female Scandinavian brown bears give birth to 1-4 cubs in January while in their den[58]. Females provide maternal care for either 1.5 or 2.5 years and family break-up generally occurs in spring soon after den emergence and before or during the mating season in May and June[59]. The mean inter-birth interval is 2.4 years in our study population, suggesting that most brown bear females that have separated from their offspring mate again in the spring and give birth to a new litter the following winter in our study population[50]. After families separate, all members may be hunted legally in the fall. Therefore, assuming no pre-weaning losses, a female using the 2.5-year tactic would be available for hunting in 1 of 3 years and her offspring could not be legally harvested as yearlings. A female using the 1.5-year tactic would be available for hunting every second year, and her yearlings would be vulnerable to harvest as well. We used data on brown bear females aged 1-24 y.o. from a long-term research project in south-central Sweden, where the recapture probability of marked females is almost 100%[28]. We focused our demographic analyses from 1993 to 2015, when the two maternal care tactics coexisted in the population. It was not possible to record data blind because our study involved marked individuals from a longitudinal long-term monitoring program and no randomization was used. Our handling of study animals was approved by the appropriate authorities and ethical committee: the Swedish Board of Agriculture (no. 35-846/03, 31-7885/07, 31-11102/12), the Uppsala Ethical Committee on Animal Experiments (no. C40/3, C47/9, C7/12), and the Swedish Environmental Protection Agency (no. 412-7327-09 Nv). We used R version 3.3.0 for all demographic and statistical analyses[60].

5.6.2 Occurrence of maternal care tactics in the population

To determine whether the relative occurrence of the 2.5-year tactic increased in the population over time, we used a binomial mixed effects model, with the probability that a litter received 2.5 years of maternal care as the response variable ("1" = received 2.5 years of maternal care, "0"= received 1.5 years of maternal care), and year as an explanatory

variable. We also included female identity as a random factor to account for multiple observations of the same mother over time.

5.6.3 Protective effect of maternal care

To determine whether being in a family group provided a survival benefit to adult females, we used a generalized linear mixed effects model and tested for the effect of female status ("in a family group" or "solitary") during the hunting season on female survival probability ("1" = survival, "0" = mortality), while controlling for female age (fixed effect) and year (random effect). For this analysis, we used all females with known reproductive status (n = 614 bear-years).

5.6.4 Tactic-based demographic analyses

To contrast fitness components and resulting demographic characteristics between maternal care tactics, we first classified females according to their tactic. Subadult females (≤3 y.o.) were classified according to the duration of maternal care they had received. Adult females (≥4 y.o.) were classified according to the maternal care tactic they used. However, such an approach is sound only if females consistently use the same maternal care tactic, i.e., if the behavior is repeatable. Therefore, we performed a GLMM-based repeatability analysis[61] on the duration of maternal care for females with at least two observed maternal care periods. A multiplicative overdispersion model for binary data with a logit function was constructed, allowing the extraction of the within-individual variance and the components of residual variance necessary for the estimation of repeatability on the latent (r_{logit}) and original ($r_{original}$) scales. However, we only present the results on the original scale. The 95% confidence intervals were constructed using a bootstrapping procedure comprising

1000 iterations. Analyses were performed using the R package "rptR"[61]. To test whether differences in maternal care tactic could be due to maternal experience, we first tested whether age differed between females using a consistent maternal care tactic and females that alternated between tactics over the study period using a Student's t-test. Second, we verified whether the probability of using either one maternal care tactic (1.5-year tactic coded "0," 2.5-year tactic coded "1") was related to female reproductive status (primiparous or multiparous) using a generalized linear mixed effects model (R package "lme4"[62]), with a binomial distribution and female identity as a random factor. In six instances, female reproductive status could not be determined and those data were removed from the above analysis. Then, females were classified into two groups according to the average duration of maternal care they provided; 13 females with average duration of maternal care ≥2 years were classified as using the 2.5-year tactic and 27 females with average duration of maternal care <2 years were classified as using the 1.5-year tactic. To increase sample size and because we found support for the repeatability of this trait, females with single reproductive events were also included in the demographic analyses and classified according to the tactic used in that event, for a total of 40 females using the 1.5-year tactic and 18 using the 2.5-year tactic.

Then, for each group of maternal care tactic, we estimated survival probability and recruitment rate (number of yearling daughters produced per year). We followed the recognized life cycle for this population with its respective age structure[34], except that our first age class was "yearling" to avoid assuming a 1:1 offspring sex-ratio in cubs-of-the-year that are not captured. The resulting population age-structure was thus: "yearling," "2 y.o.," "3 y.o.," "4-8 y.o.," and "9+ y.o." (Appendix 5.1: Figure A5.1). We estimated survival for females within those five age classes. Fecundity represents the probability that a female survives and reproduces the next year (i.e., $\text{Fecundity}_t = \text{Survival}_{(t \rightarrow t+1)} \times \text{Recruitment}_{t+1}$). Therefore, we estimated recruitment for age classes 5-9 and 10+ y.o. to follow age classes for survival and because 5 y.o. is the youngest age at which females may

start producing yearlings. Sample sizes used to estimate each tactic- and age classspecific demographic rates are presented in Appendix 5.1: Table A5.1.

Survival probability ("1" = survival, "0" = mortality) and recruitment (range: 0-3 yearling daughters per year) of females were compared between tactics and age classes using binomial and negative binomial (R packages "lme4" and "blme"[63]) generalized linear mixed effects models, respectively. We added an interaction between tactic and age class to compare within-age-class differences in survival, with year as a random effect. Female identity was added as a random effect in models of recruitment to account for multiple observations of the same females. Parameter significance tests and model simplifications were performed with likelihood ratio tests. Homoscedasticity was checked by plotting the residuals of the models. The resulting models were used to generate bootstrapped (10,000 iterations) tactic- and age-specific predictions of survival probability and recruitment to generate 95% confidence intervals using the R package "lme4"[62].

To estimate asymptotic population growth rate, λ, a proxy of fitness, for each maternal care tactic, we inserted these tactic- and age-specific model predictions for survival probability and recruitment into two different population models, one for each tactic. We constructed two 9 x 9 female-based Leslie population matrix models ($\mathbf{A}_{1.5}$ and $\mathbf{A}_{2.5}$) comprising the five previously described age classes. For ages between 4 and 8, we added separated columns and rows even if single survival probabilities and fecundity were calculated for these age classes, resulting in 9 x 9 rather than 5 x 5 matrices, as follows:

$$\mathbf{A}_{1.5} = \begin{bmatrix} 0 & 0 & 0 & F_{4-8,1.5} & F_{4-8,1.5} & F_{4-8,1.5} & F_{4-8,1.5} & F_{4-8,1.5} & F_{9+,1.5} \\ S_{1,1.5} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{2,1.5} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{3,1.5} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{4-8,1.5} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{4-8,1.5} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{4-8,1.5} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{4-8,1.5} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{4-8,1.5} & S_{9+,1.5} \end{bmatrix};$$

$$\mathbf{A}_{2.5} = \begin{bmatrix} 0 & 0 & 0 & F_{4-8,2.5} & F_{4-8,2.5} & F_{4-8,2.5} & F_{4-8,2.5} & F_{4-8,2.5} & F_{9+,2.5} \\ S_{1,2.5} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{2,2.5} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{3,2.5} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{4-8,2.5} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{4-8,2.5} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{4-8,2.5} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_{4-8,2.5} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{4-8,2.5} & S_{9+,2.5} \end{bmatrix}$$

This prevented us from having to attribute a fixed proportion of individuals transiting between the two age classes over time. The matrices were used to extract the dominant eigenvalue, i.e., the asymptotic population growth rate (λ) for each tactic. As a second measure of fitness, we also extracted the net reproductive rate (R_0), which corresponds to the number of females an individual is expected to produce over its lifetime. Apart from these fitness-related measures, we calculated the generation time (T) and stable age structure of each maternal care tactic to provide a demographic comparison of theoretical populations consisting of either one of the two maternal care tactics. All fitness and demographic metrics were calculated using the R package "popbio"[64]. For each tactic-based

matrix model, we recalculated these metrics using bootstrapped model predictions for all survival probabilities and recruitment values to generate 95% confidence intervals.

5.6.5 Differential effects of hunting between tactics

To assess the influence of hunting pressure on the fitness of maternal care tactics, we first estimated an annual index of hunting pressure. This index was calculated by dividing the number of marked bears shot in a given year by the number of marked bears available for hunting that same year, i.e., the probability that a marked bear available for hunting was shot (Appendix 5.1: Figure A5.2). Individuals within family groups are not available for hunting and thus were not considered in the index. Similarly, we excluded individuals that died before the onset of the hunting season.

Then, we modeled the effect of hunting pressure on each survival probability independently using Bayesian models with the R package "MCMCglmm"[65] with uninformative inverse-Wishart priors, 2,600,000 iterations, a thinning of 2500 and a burnin of 100,000. In these models, survival ("1" = survival, "0" = death) was set as response variable and hunting pressure as the explanatory variable. Effect sizes (log-odds) of hunting on the survival probabilities of each maternal care tactic and each age-class are presented in Appendix 5.1: Table A5.2. We used these models to generate 1000 posterior predictions for each survival estimate over the range of hunting pressures observed (12 values of hunting pressure ranging between 0 and 0.33). These predictions were back-transformed on the original scale and introduced in the previously built tactic-specific matrix models. We repeated this procedure using the 95% posterior distribution of parameter estimates. This produced a posterior distribution of predicted λ for each simulated hunting pressure and each maternal care tactic.

To tease apart the effect of hunting pressure from other potential densityrelated factors, we have conducted similar simulations using a population density index derived from county-level scat collection conducted in Sweden[66]. The weighted values of individual bear scat locations were summed in 10 km x 10 km cells to produce spatially explicit bear densities. These densities were then corrected for temporal variations using the Large Carnivore Observation Index[66]. Finally, annual density cells were summed over the study area and scaled (from 0 to 1) to obtain an index of annual density that reflects temporal changes in bear population density[43,44]. As for hunting pressure, effect sizes (log-odds) of density (Appendix 5.1: Table A5.3) on survival components were then used to generate posterior predictions of λ dependent on population density index. However, the derived bear density index was only available for the period 1998 2015. Therefore, we also re-ran the simulations on hunting pressure, but this time only predicting λ for the hunting pressures encountered during the period 1998-2015, when both indexes of hunting pressure and population density were available. We then generated model predictions for tactic- and age class-specific survival probabilities for 12 values of hunting pressure and population density observed in the population during the period 1998-2015 (Appendix 5.1: Table A5.3 and Figure A5.3).

5.7 Data availability

The data used in this study are fully available upon request from the corresponding authors.

5.8 Acknowledgments

We thank R. Bischof, G. Blanchet, and D. Gravel for their advice and comments. We thank M. Festa-Bianchet and M. Leclerc for their comments on earlier versions of the manuscript.

We are also grateful to S. Frank for his help with the index of bear population density. J.V.d.W. was financially supported by the Fonds de Recherche du Québec- Nature et Technologies (grant number: 184518) and by the Natural Sciences and Engineering Research Council of Canada (NSERC grant number: PGSD2-504356-2017). G.P. and F.P. were funded by NSERC discovery grant and by the Canada Research Chair in Evolutionary Demography and Conservation. This is scientific paper number 248 from the Scandinavian Brown Bear Research Project, which is funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Austrian Science Fund, and the Swedish Association for Hunting and Wildlife Management. We acknowledge the support of the Center for Advanced Study in Oslo, Norway, that funded and hosted our research project "Climate effects on harvested large mammal populations" during the academic year of 2015-2016 and funding from the Polish-Norwegian Research Program operated by the National Center for Research and Development under the Norwegian Financial Mechanism 2009-2014 in the frame of Project Contract No POL-NOR/198352/85/2013.

5.9 Author contributions

J.V.d.W., F.P., A.Z. and J.E.S. have conceived the idea, J.V.d.W. and G.P. realized the analyses, J.V.d.W. wrote the first version of the manuscript and all authors have contributed to the subsequent versions of the manuscript. F.P. and A.Z. supervised the study. J.E.S. and A.Z. coordinated the Scandinavian Brown Bear Research Project.

5.10 Competing interests

The authors declare no competing interests.

5.11 References

1. Darimont, C. T. *et al.* Human predators outpace other agents of trait change in the wild. *Proc. Natl. Acad. Sci. USA* **106**, 952–954 (2009).

2. Lambert, Y. Long-term changes in life history characteristics and reproductive potential of northern Gulf of St. Lawrence cod (*Gadus morhua*) and consequences for the stock productivity. *Fish. Res.* **138**, 5–13 (2013).

3. Law, R. Fisheries-induced evolution: present status and future directions. *Mar. Ecol. Prog. Ser.* **335**, 271–277 (2007).

4. Jørgensen, C. et al. Managing evolving fish stocks. *Science* **318**, 1247–1248 (2007).

5. Law, R. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* **57**, 659–668 (2000).

6. Pigeon, G., Festa-Bianchet, M., Coltman, D. W. & Pelletier, F. Intense selective hunting leads to artificial evolution in horn size. *Evol. Appl.* **9**, 521–530 (2016).

7. Coltman, D. W. et al. Undesirable evolutionary consequences of trophy hunting. *Nature* **426**, 655–658 (2003).

8. Allendorf, F. W. & Hard, J. J. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proc. Natl. Acad. Sci. USA* **106**, 9987–9994 (2009).

9. Mysterud, A. Selective harvesting of large mammals: how often does it result in directional selection? *J. Appl. Ecol.* **48**, 827–834 (2011).

10. Thelen, T. H. Effects of harvest on antlers of simulated populations of elk. *J. Wildl. Manag.* **55**, 243–249 (1991).

11. Proaktor, G., Coulson, T. & Milner-Gulland, E. J. Evolutionary responses to harvesting in ungulates. *J. Anim. Ecol.* **76**, 669–678 (2007).

12. Law, R. & Grey, D. R. Evolution of yields from populations with age-specific cropping. *Evol. Ecol.* **3**, 343–359 (1989).

13. Engen, S., Lande, R. & Sæther, B.-E. Evolutionary consequences of nonselective harvesting in density-dependent populations. *Am. Nat.* **184**, 714–726 (2014).

14. Bunnefeld, N., Baines, D., Newborn, D. & Milner-Gulland, E. J. Factors affecting unintentional harvesting selectivity in a monomorphic species. *J. Anim. Ecol.* **78**, 485–492 (2009).

15. Heino, M., Pauli, B. D. & Dieckmann, U. Fisheries-induced evolution. *Annu. Rev. Ecol. Evol. Syst.* **46**, 461–480 (2015).

16. Tiilikainen, R., Nygrén, T., Pusenius, J. & Ruusila, V. Variation in growth pattern of male moose *Alces alces* after two contrasted periods of hunting. *Ann. Zool. Fennn.* **47**, 159–172 (2010).

17. Stearns, S. C. *The evolution of life histories.* (Oxford University Press, Oxford, 1992).

18. Servanty, S. et al. Influence of harvesting pressure on demographic tactics: implications for wildlife management. *J. Appl. Ecol.* **48**, 835–843 (2011).

19. Leclerc, M., Zedrosser, A. & Pelletier, F. Harvesting as a potential selective pressure on behavioural traits. *J. Appl. Ecol.* **54**, 1941–1945 (2017).

20. Festa-Bianchet, M. in *Animal behavior and wildlife conservation* (eds. Festa-Bianchet, M. & Apollonio, M.) 191–207 (Island Press, Washington, DC, 2003).

21. Rughetti, M. & Festa-Bianchet, M. Effects of early horn growth on reproduction and hunting mortality in female chamois. *J. Anim. Ecol.* **80**, 438–447 (2011).

22. Krofel, M., Jonozovič, M. & Jerina, K. Demography and mortality patterns of removed brown bears in a heavily exploited population. *Ursus* **23**, 91–103 (2012).

23. McLellan, B. N. & Shackleton, D. M. A comparison of grizzly bear harvest data from Montana and southeastern British Columbia. *Wildl. Soc. Bull.* **16**, 371–375 (1988).

24. Solberg, E. J., Loison, A., Saether, B.-E. & Strand, O. Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildl. Biol.* **6**, 41–52 (2000).

25. Rughetti, M. & Festa-Bianchet, M. Effects of selective harvest of non-lactating females on chamois population dynamics. *J. Appl. Ecol.* **51**, 1075–1084 (2014).

26. Ericsson, G. Reduced cost of reproduction in moose *Alces alces* through human harvest. *Alces* **37**, 61–69 (2001).

27. Zedrosser, A., Pelletier, F., Bischof, R., Festa-Bianchet, M. & Swenson, J. E. Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations. *Ecology* **94**, 231–240 (2013).

28. Bischof, R., Swenson, J. E., Yoccoz, N. G., Mysterud, A. & Gimenez, O. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *J. Anim. Ecol.* **78**, 656–665 (2009).

29. Dahle, B. & Swenson, J. E. Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring. *Behav. Ecol. Sociobiol.* **54**, 352–358 (2003).

30. Balme, G. A., Robinson, H. S., Pitman, R. T. & Hunter, L. T. B. Flexibility in the duration of parental care: female leopards prioritise cub survival over reproductive output. *J. Anim. Ecol.* **86**, 1224–1234 (2017).

31. Mylius, S. D. & Diekmann, O. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. *Oikos* **74**, 218–224 (1995).

32. Sibly, R. M. & Hone, J. Population growth rate and its determinants: an overview. *Philos. Trans. R. Soc. Lond. B* **357**, 1153–1170 (2002).

33. Caswell, H. *Matrix population models: construction, analysis, and interpretation.* (Sinauer Associates, Sunderland, MA, 2001).

34. Gosselin, J., Zedrosser, A., Swenson, J. E. & Pelletier, F. The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. *Proc. R. Soc. B* **282**, 20141840 (2015).

35. Milner, J. M., Nilsen, E. B. & Andreassen, H. P. Demographic side effects of selective hunting in ungulates and carnivores. *Conserv. Biol.* **21**, 36–47 (2007).

36. Sæther, B.-E. et al. How life history influences population dynamics in fluctuating environments. *Am. Nat.* **182**, 743–759 (2013).

37. Gaillard, J.-M. & Yoccoz, N. G. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* **84**, 3294–3306 (2003).

38. Gittleman, J. L. & Thompson, S. D. Energy allocation in mammalian reproduction. *Am. Zool.* **28**, 863–875 (1988).

39. Zedrosser, A., Steyaert, S. M. J. G., Gossow, H. & Swenson, J. E. Brown bear conservation and the ghost of persecution past. *Biol. Conserv.* **144**, 2163–2170 (2011).

40. Swenson, J. E. et al. Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. *Wildl. Biol.* wlb.00251 (2017).

41. Sinervo, B., Svensson, E. & Comendant, T. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**, 985–988 (2000).

42. Swenson, J. E., Dahle, B. & Sandegren, F. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* **12**, 81–92 (2001).

43. Frank, S. C. et al. Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. *J. Anim. Ecol.* **87**, 247–258 (2018).

44. Leclerc, M., Frank, S. C., Zedrosser, A., Swenson, J. E. & Pelletier, F. Hunting promotes spatial reorganization and sexually selected infanticide. *Sci. Rep.* **7**, 45222 (2017).

45. Cam, E. & Aubry, L. Early development, recruitment and life history trajectory in long-lived birds. *J. Ornithol.* **152**, S187–S201 (2011).

46. Lee, P. C., Majluf, P. & Gordon, I. J. Growth, weaning and maternal investment from a comparative perspective. *J. Zool. Lond.* **225**, 99–114 (1991).

47. Hertel, A. G. et al. Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos* **127**, 197–207 (2018).

48. Stenset, N. E. et al. Seasonal and annual variation in the diet of brown bears *Ursus arctos* in the boreal forest of southcentral Sweden. *Wildl. Biol.* **22**, 107–116 (2016).

49. Schwartz, C. C., Miller, S. D. & Haroldson, M. A. in *Wild mammals of North America: biology, management and conservation* (eds. Feldhammer, G. A., Thompson, B. C. & Chapman, J. A.) 556–586 (The John Hopkins University Press, Baltimore, MD, 2003).

50. Nawaz, M. A., Swenson, J. E. & Zakaria, V. Pragmatic management increases a flagship species, the Himalayan brown bears, in Pakistan's Deosai National Park. *Biol. Conserv.* **141**, 2230–2241 (2008).

51. Smallegange, I. M. & Coulson, T. Towards a general, population-level understanding of eco-evolutionary change. *Trends Ecol. Evol.* **28**, 143–148 (2013).

52. Lindsey, P. A. et al. The trophy hunting of African lions: scale, current management practices and factors undermining sustainability. *PLOS One* **8**, e73808 (2013).

53. Czetwertynski, S. M., Boyce, M. S. & Schmiegelow, F. K. Effects of hunting on demographic parameters of American black bears. *Ursus* **18**, 1–18 (2007).

54. Lee, P. C. & Moss, C. J. Early maternal investment in male and female African elephant calves. *Behav. Ecol. Sociobiol.* **18**, 353–361 (1986).

55. Derocher, A. E., Andriashek, D. & Arnould, J. P. Y. Aspects of milk composition and lactation in polar bears. *Can. J. Zool.* **71**, 561–567 (1993).

56. Borries, C., Lu, A., Ossi-Lupo, K., Larney, E. & Koenig, A. The meaning of weaning in wild Phayre's leaf monkeys: last nipple contact, survival, and independence. *Am. J. Phys. Anthropol.* **154**, 291–301 (2014).

57. Bischof, R., Fujita, R., Zedrosser, A., Söderberg, A. & Swenson, J. E. Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. *J. Wildl. Manag.* **72**, 79–88 (2008).

58. Friebe, A., Swenson, J. E. & Sandegren, F. Denning chronology of female brown bears in central Sweden. *Ursus* **12**, 37–46 (2001).

59. Dahle, B. & Swenson, J. E. Family break-up in brown bears: are young forced to leave? *J. Mammal.* **84**, 536–540 (2003).

60. R: A language and environment for statistical computing. (R Core Team, 2016).

61. Nakagawa, S. & Schielzeth, H. Repeatability for Gaussian and non-Gaussian data : a practical guide for biologists. *Biol. Rev.* **85**, 935–956 (2010).

62. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).

63. Chung, Y., Rabe-Hesketh, S., Dorie, V., Gelman, A. & Liu, J. A nondegenerate penalized likelihood estimator for variance parameters in multilevel models. *Psychometrika* **78**, 685–709 (2013).

64. Stubben, C. & Milligan, B. Estimating and analyzing demographic models using the popbio package in R. *J. Stat. Softw.* **22**, 1–23 (2007).

65. Hadfield, J. D. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* **33**, 1–22 (2010).

66. Kindberg, J. et al. Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildl. Biol.* **17**, 114–123 (2011).

CHAPITRE 6
DISCUSSION ET CONCLUSION

6.1 Retour sur les objectifs et les résultats de la thèse

L'objectif principal de ma thèse était de mieux comprendre les tactiques de reproduction maternelles et, plus particulièrement, d'identifier les causes et les conséquences de la variation dans la durée des soins maternels. Je me suis intéressée à la période de soins maternels, une période cruciale pour le développement et la survie des jeunes, mais aussi très énergivore pour les femelles. La quantité de soins, ou la durée de la période de soins, se doit donc d'être un compromis entre les intérêts de la progéniture et ceux de la mère (Williams, 1966; Stearns, 1992). Ma thèse, utilisant l'ours brun scandinave comme modèle d'étude, a permis de montrer que les coûts et les bénéfices associés aux soins maternels sont muables; ils peuvent varier d'un individu et d'un contexte à l'autre.

Au chapitre 2, j'ai montré que les soins maternels ne sont pas distribués de façon homogène entre les jeunes d'une même portée. Je me suis intéressée à la relation négative existant entre la masse des jeunes et le nombre de jeunes produits au cours d'un même évènement de reproduction (Charnov et Ernest, 2006). Mes résultats montrent que, dans les plus grandes portées, seuls les plus petits oursons ont une masse réduite. Les femelles transféreraient ainsi le coût de la reproduction à certains de leurs oursons et maintiendraient un investissement stable dans les plus gros oursons, selon une tactique de reproduction conservatrice. Cette étude souligne l'importance de considérer l'hétérogénéité phénotypique au sein des portées dans l'évaluation des compromis d'histoire de vie et les tactiques de reproduction maternelles.

Au chapitre 3, j'ai exploré les déterminants intrinsèques de la durée des soins maternels dans deux populations suédoises d'ours brun (le nord et le sud). J'ai montré, par l'identification de liens de causalité, que les déterminants de la durée des soins maternels étaient contexte-dépendants. En effet, à l'échelle de la Suède, la durée des soins maternels était causée directement par la taille de portée, la masse et l'âge de la mère, mais pas par la masse des jeunes. Toutefois, la durée des soins maternels n'était affectée directement que par la masse des jeunes dans le nord et par l'âge de la mère dans le sud. La différence s'expliquerait par les différentes pressions environnementales, dont l'intensité de la chasse réglementée, sévissant dans les deux populations. Cette étude empirique apporte une importante contribution à notre compréhension jusqu'alors très limitée des causes de variation dans la durée des soins maternels en milieu naturel.

Au chapitre 4, j'ai étudié le rôle des conflits sexuels dans la durée des soins maternels. On oublie souvent de considérer les intérêts des mâles dans la dynamique mère-jeune chez les espèces où les mâles ne fournissent pas de soins parentaux. Les mâles peuvent forcer la séparation de groupes familiaux, forcer le retour en œstrus des femelles et ainsi devenir, plus rapidement, les géniteurs de la prochaine portée (Hrdy, 1979). J'ai montré que les femelles fournissant de longs soins maternels ont des comportements d'évitement des mâles durant la période de reproduction, là où le risque de séparation des groupes familiaux est grand (Dahle et Swenson, 2003b; Gosselin *et al.*, 2017). Elles sélectionneraient des habitats près des habitations humaines, ce qui leur servirait de bouclier contre des interactions agressives avec des mâles et permettrait de poursuivre les soins maternels. Cette étude apporte une contribution importante en encourageant l'intégration des conflits sexuels dans l'évaluation des tactiques de reproduction maternelles.

Finalement, au chapitre 5, j'ai étudié la sélection induite par la chasse et sa réglementation comme contexte environnemental pouvant influencer la durée des soins maternels. J'ai montré que la réglementation de la chasse interdisant de tuer des membres de groupes

familiaux procure artificiellement un bénéfice en survie aux femelles prodiguant des soins maternels longs et sélectionnerait pour de plus longs soins maternels dans la population. Ce changement en tactiques de reproduction pourrait avoir des conséquences démographiques via une modification de la structure d'âge et du temps de génération de la population. Ce chapitre apporte une importante contribution à notre compréhension des effets indirects de la chasse sur les populations animales sauvages.

De façon générale, mes recherches apportent une importante contribution à notre compréhension des tactiques de reproduction maternelles en montrant empiriquement comment ces dernières sont modulées par l'hétérogénéité individuelle et le contexte environnemental chez les mammifères. Par exemple, les résultats des chapitres 4 et 5 ont montré que la présence de l'Homme et ses activités ont le potentiel d'influencer les tactiques de reproduction maternelles en milieu sauvage. La plus importante contribution de ma thèse est l'exploration des déterminants intrinsèques et contextuels de la durée des soins maternels et l'évaluation des conséquences individuelles et populationnelles de la variation dans ce trait d'histoire de vie. En effet, comprendre les causes de variation dans les traits liés à la reproduction et leurs impacts démographiques est primordial pour anticiper la réponse des populations animales sauvages face aux pressions environnementales grandissantes.

6.2 La meilleure tactique de reproduction dépend du contexte

La meilleure tactique de reproduction maternelle devrait viser une optimisation du ratio bénéfices/coûts pour les femelles (Williams, 1966). Dans le nord de la Suède, les conditions environnementales sont plus difficiles que dans le sud; l'hiver est plus long (Dahle et al. 2006) et froid et la saison de croissance de la végétation est plus courte, ce qui réduit la productivité primaire (Zedrosser et al. 2006). Ainsi, les femelles adultes y sont

plus petites et leur masse est plus affectée par des fluctuations annuelles dans l'abondance de la nourriture dans le nord que dans le sud de la Suède (Zedrosser et al. 2006). Une prolongation de la durée des soins maternels impliquerait alors potentiellement des coûts plus importants pour les femelles dans le nord que dans le sud. Compte tenu que la masse des jeunes est la principale cause de variation dans la durée des soins maternels dans le nord (chapitre 3), la stratégie de reproduction serait ainsi de moduler la durée des soins maternels en fonction de la condition des jeunes. Prodiguer des soins courts lorsque les jeunes sont assez gros procure le bénéfice d'un retour rapide à la reproduction (Lee *et al.*, 1991), tout en maximisant les chances de survie des oursons et en minimisant les coûts associés à une prolongation des soins maternels. À l'inverse, prodiguer des soins longs pourrait compenser pour la plus faible masse des oursons (Dahle et Swenson, 2003c) et augmenter ainsi leurs chances de survie, ce qui procurerait un bénéfice indirect suffisant pour compenser les coûts en perte de reproduction associés.

Dans le sud de la Suède, mes résultats suggèrent que la meilleure tactique de reproduction ne dépend pas de la condition des jeunes (chapitre 3). Alors, qu'est-ce qui détermine la durée des soins maternels dans le sud? La qualité et la quantité de données disponibles dans le sud nous ont permis de tester des hypothèses alternatives. La durée des soins maternels pourrait être expliquée par le comportement de sélection d'habitat des femelles (chapitre 4) et la sélection induite par la chasse et sa réglementation (chapitre 5). Les femelles sélectionnant des habitats similaires aux mâles auraient plus de chances de rencontrer des mâles durant la période d'accouplements, ce qui induirait une séparation hâtive des groupes familiaux. Dans ce contexte, les femelles n'auraient pas l'opportunité d'exprimer la tactique de reproduction optimale, et seraient plutôt victimes du conflit sexuel. La durée des soins maternels semble donc aussi tributaire des agents extérieurs et le rôle des mâles est potentiellement plus grand que ce que l'on envisageait. Ceci est d'autant plus vrai que, dans le sud, le fort prélèvement de mâles à la chasse créé des espaces libres dans le paysage qui favorisent les déplacements des mâles voisins survivants et les rencontres potentiellement agressives entre ces mâles et les femelles (Leclerc *et al.*, 2017a; Gosselin *et al.*, 2017). En

contrepartie, les contre-stratégies utilisées par les femelles, telle que l'évitement des mâles par ségrégation spatiale (chapitre 4), pourraient permettre aux femelles de regagner un « pouvoir décisionnel » sur leur investissement dans la reproduction (Palombit, 2015).

De plus, la forte présence de l'Homme et de ses activités dans le sud semble perturber la balance entre les coûts et bénéfices associés aux différentes durées des soins maternels. Effectivement, on attribue le taux de croissance élevé de la population d'ours brun scandinave (Saether *et al.*, 1998) à la forte persécution passée qui aurait entraîné une accélération de sa vitesse d'histoire de vie, comparativement aux autres populations d'ours brun (Nawaz *et al.*, 2008; Zedrosser *et al.*, 2011). À cette époque, où la chasse était forte et aléatoire, des soins maternels courts était probablement sous pression de sélection. De nos jours, la croissance de la population a beaucoup ralenti (Swenson *et al.*, 2017) et un retour à des durées de soins maternels plus représentatives des autres populations d'ours brun mondialement est possible. De plus, dans le contexte actuel de chasse intensive et non-aléatoire, les coûts associés à de plus longs soins maternels sont largement réduits artificiellement, voir même remplacés par des bénéfices en survie pour les femelles et les oursons. Alors qu'on attribue généralement la tactique de reproduction 2,5 ans à des femelles de moins bonne « qualité », il semblerait que dans un contexte de chasse intensive et sélective, il s'agit de la meilleure tactique de reproduction (Van de Walle *et al.*, 2018). En fonction de changements temporels dans la population, la sélection naturelle peut effectivement favoriser des tactiques de reproduction alternatives (Sinervo *et al.*, 2000).

6.3 Effets indirects et insoupçonnés de la chasse sur les traits reproducteurs

À l'ère de l'Anthropocène, l'activité humaine, dont la surexploitation, est l'un des plus grands agents de changements environnementaux et phénotypiques en milieu naturel (Palumbi, 2001; Darimont *et al.*, 2009; Pelletier et Coltman, 2018). En Suède, on a

répertorié les effets directs et indirects observés et potentiels de la forte pression de prédation par l'Homme sur l'ours brun (Frank *et al.*, 2017). Les principaux effets documentés à ce jour concernent les traits comportementaux (Hertel *et al.*, 2016; Steyaert *et al.*, 2016; Leclerc *et al.*, 2017a; 2019; Gosselin *et al.*, 2017). Bien que des changements dans les comportements puissent avoir des conséquences indirectes sur le taux de croissance de la population (Gosselin *et al.*, 2015), les changements induits par l'Homme sur les traits d'histoire de vie ont un plus grand potentiel d'influencer la dynamique de la population (Bischof *et al.*, 2018). Ainsi, il était donc important, d'un point de vue de gestion de la faune, d'apporter une quantification des effets indirects de la chasse sur la durée des soins maternels.

Là où elle est implantée, la réglementation de la chasse interdisant de tuer des femelles ou des membres de groupes familiaux vise à protéger le segment femelle de la population et ainsi minimiser l'impact de la chasse sur le taux de croissance de la population (Miller, 1990). Je montre que cette réglementation entraîne toutefois l'effet insoupçonné d'augmenter la probabilité de survie des femelles prodiguant des soins maternels longs avec des conséquences démographiques. En Scandinavie, la protection des groupes familiaux est réglementée légalement. Une réglementation similaire est aussi en vigueur dans plusieurs autres populations d'ours (McLellan et Shackleton, 1988; Kohlmann *et al.*, 1999; Mclellan *et al.*, 1999; Krofel *et al.*, 2012). On pourrait donc s'attendre à des effets similaires dans d'autres populations ou chez d'autres espèces. Par exemple, en Suède, la protection légale des femelles orignal (*Alces alces*) accompagnées de faons réduirait les coûts de la reproduction pour les femelles (Ericsson, 2001). En créant un biais dans la récolte vers les mâles et les femelles non-reproductrices (McLellan et Shackleton, 1988; Bischof *et al.*, 2009), cette réglementation pourrait aussi déstabiliser la structure de sexe et d'âge de la population avec des conséquences indirectes sur la dynamique de population qu'il serait pertinent d'évaluer. De surcroît, il est important de considérer que même en absence de règlements et de sanctions, les chasseurs montrent une grande réticence à tuer des femelles accompagnées de jeunes en vertu de considérations éthiques. Cette réticence

peut suffire à créer un biais dans les individus récoltés en faveur des femelles non-reproductrices et des mâles et affecter la composition de la population (Rughetti et Festa-Bianchet, 2014). Mes résultats ont donc une portée beaucoup plus large et peuvent s'appliquer à nombre de populations animales sauvages subissant une forte pression de chasse. La sélection pourrait alors s'appliquer à tout trait ayant le potentiel de fournir une forme de protection, tel que l'âge à la première reproduction et la probabilité de conception. L'intensité de la sélection sur ces traits dépendrait de l'intensité de la chasse et de l'habileté des chasseurs à discerner le sexe des individus et leur statut reproducteur sur le terrain (Festa-Bianchet, 2003; Bischof *et al.*, 2009).

6.4 Changements temporels dans la durée des soins maternels : évolution?

Au chapitre 5, j'ai montré que, depuis les 20 dernières années, la durée moyenne des soins maternels a augmenté dans la population d'ours brun au sud de la Suède. En effet, la première portée ayant reçu 2,5 ans de soins maternels a été observée en 1995 et, depuis ce temps, environ 25 % des portées ont reçu 2,5 ans de soins maternels (Van de Walle *et al.*, 2018). Bien que des changements dans la condition corporelle des femelles et des oursons ont été rapportés (Leclerc *et al.*, 2016), mes résultats suggèrent que le changement temporel dans la durée des soins maternels ne serait pas dû à une diminution de la masse des mères et des oursons (chapitre 3). La sélection induite par la chasse constituerait peut-être un élément de réponse pour expliquer ce changement temporel. Les femelles procurant des soins maternels courts se retrouvent plus souvent solitaires durant la période de chasse et ainsi plus vulnérables à la chasse. Compte-tenu qu'environ 30 % des ours disponibles à la chasse sont tués à chaque automne (Figure 1.5), cela représente un important filtre démographique retirant disproportionnellement les femelles utilisant la tactique 1,5 ans. Ce filtre démographique pourrait expliquer la diminution de l'occurrence de la tactique 1,5 ans au profit de la tactique 2,5 ans au cours des 20 dernières années dans la population.

La pression exercée par la récolte peut induire des changements évolutifs dans les populations animales sauvages (Harris *et al.*, 2002; Chiyo *et al.*, 2015; Pigeon *et al.*, 2016). Tel que mentionné au chapitre 1, d'après Darwin (1859), les changements évolutifs peuvent survenir lorsque trois conditions sont remplies : 1) il existe de la variation phénotypique entre les individus (variabilité), 2) la valeur adaptative des individus varie en fonction des différents phénotypes qu'ils expriment (sélection) et 3) les traits phénotypiques possèdent une base génétique (héritabilité). Dans ma thèse, j'ai montré que la durée des soins maternels est variable entre les individus (condition 1) et que la valeur adaptative des femelles diffère en fonction de la durée de soins maternels qu'elles prodiguent (condition 2). La condition 3 doit toutefois être satisfaite pour déterminer si les changements phénotypiques actuellement observés chez l'ours brun scandinave sont évolutifs et si le maintien de la forte pression de sélection induite par la chasse et sa réglementation pourrait mener à des changements évolutifs dans le futur.

Au chapitre 5, j'ai montré que la durée des soins maternels était un trait répétable à 33 %. La répétabilité est la limite supérieure possible de l'héritabilité (Falconer et Mackay, 1996), ce qui suggère une héritabilité possible de la durée des soins maternels entre 0 % et 33 %. Les traits d'histoire de vie sont souvent canalisés par sélection naturelle vers une valeur optimale, ce qui érode la variation naturelle dans ces traits (Falconer et Mackay, 1996; Kruuk *et al.*, 2000) et explique les faibles valeurs d'héritabilité généralement associées à ces traits ($\bar{x}$ = 0.33), comparativement aux traits morphologiques ($\bar{x}$ = 0.56), comportementaux ($\bar{x}$ = 0.52) et physiologiques ($\bar{x}$ = 0.49; Postma, 2014). Toutefois, lorsque la pression de sélection est forte et constante, l'évolution sur les traits d'histoire de vie (p. ex. âge à la maturation) peut être observée (Jørgensen *et al.*, 2007; Allendorf et Hard, 2009). Il existe actuellement un pédigrée de la population d'ours brun au sud de la Suède et ce dernier s'est avéré utile pour estimer l'apparentement entre les individus (Frank *et al.*, 2018) et l'héritabilité de la circonférence de la tête (Rivrud *et al.*, 2019) grâce à un modèle animal (Wilson *et al.*, 2010). Le pédigrée (voir matériel supplémentaire S2 dans Frank *et al.*, 2018) contient un total de 1463 jeunes avec 776 mères connues ou assignées

génétiquement (assignation maternelle totale = 53 %) et 734 pères assignés génétiquement (assignation paternelle = 50 %). Toutefois, la puissance du pédigrée actuel pour détecter statistiquement des valeurs d'héritabilité de l'ordre de celles attendues pour les traits d'histoire de vie avec un modèle animal est faible (Figure 6.1; A. Bourret, données non publiées). De plus, la nature dichotomique du trait « durée des soins maternels » pourrait diminuer davantage notre capacité statistique à détecter une valeur d'héritabilité pour ce trait.

Outre les analyses de génétique quantitative, l'héritabilité des traits peut être estimée grâce à des régressions parents-enfants (p. ex. Réale et Festa-Bianchet, 2000). Avec cette méthode, la valeur du trait des enfants (variable réponse) est mise en relation avec la valeur du trait des parents (variable explicative). La pente de la régression linéaire correspond à une approximation de la valeur d'héritabilité (h^2) dans le cas des relations parents-enfants, et à $½h^2$ dans les cas des relations mère-fille (Falconer et Mackay, 1996). Malgré que j'aie estimé un total de 152 durées de soins maternels chez l'ours brun dans le sud de la Suède, seuls 41 couples mère-fille ont pu être établis sur la base de cet échantillon. La relation mère-filles (moyenne de la mère *vs* moyenne de ses filles, n = 26) n'était pas significative (Figure 6.2), ce qui suggère que la durée des soins maternels n'est pas héritable ou alors que nous ne disposons pas d'une puissance statistique suffisante pour estimer l'héritabilité de ce trait. Il est très difficile d'obtenir une grande taille d'échantillon sur la durée des soins maternels. En effet, pour qu'une durée de soins maternels soit estimée, une femelle doit survivre jusqu'à l'âge de reproduction et produire une portée viable. En Scandinavie, l'âge moyen de la mort des femelles (4,8 ans; Zedrosser *et al.*, 2013) est inférieur à l'âge moyen de la première reproduction avec succès (5,4 ans; Zedrosser *et al.*, 2009) et la probabilité de survie des oursons de l'année est aussi faible, soit de 60 % (Gosselin *et al.*, 2015). Un autre élément à considérer et la relativement récente augmentation dans la durée des soins maternels où l'occurrence des soins maternels longs n'est importante (environ 36 %) que depuis 2005 (Van de Walle *et al.*, 2018). Si l'on considère que le temps de génération est d'environ 9-12 ans (Van de Walle *et al.*, 2018), on commence à peine à obtenir des

informations sur la reproduction des filles ayant reçu des soins maternels longs. Il serait pertinent de re-tester la régression mère-fille dans quelques années et avec une taille d'échantillon bonifiée.

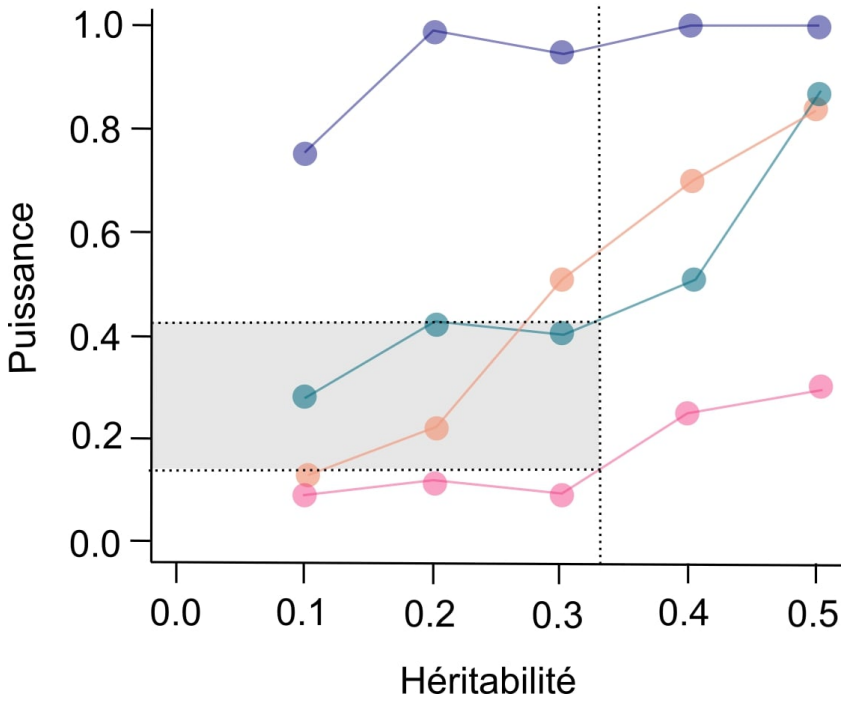

Figure 6.1 **Analyses de puissance du potentiel de détection de valeurs d'héritabilités simulées en utilisant le pédigrée de l'ours brun scandinave dans le sud de la Suède, pour les traits morphologiques (violet), comportementaux (orange) et d'histoire de vie (taille de portée; vert, âge à la première reproduction; rose).**

Les points représentent la moyenne sur 100 répétitions. Données fournies et analyses réalisées par A. Bourret, 2016, avec la librairie R « pedantics ». La ligne verticale pointillée correspond à la répétabilité de la durée des soins maternels, soit la valeur maximale potentielle de l'héritabilité pour ce trait. Les lignes horizontales pointillées délimitent l'étendue de la puissance statistique maximale pour détecter ce trait d'histoire de vie.

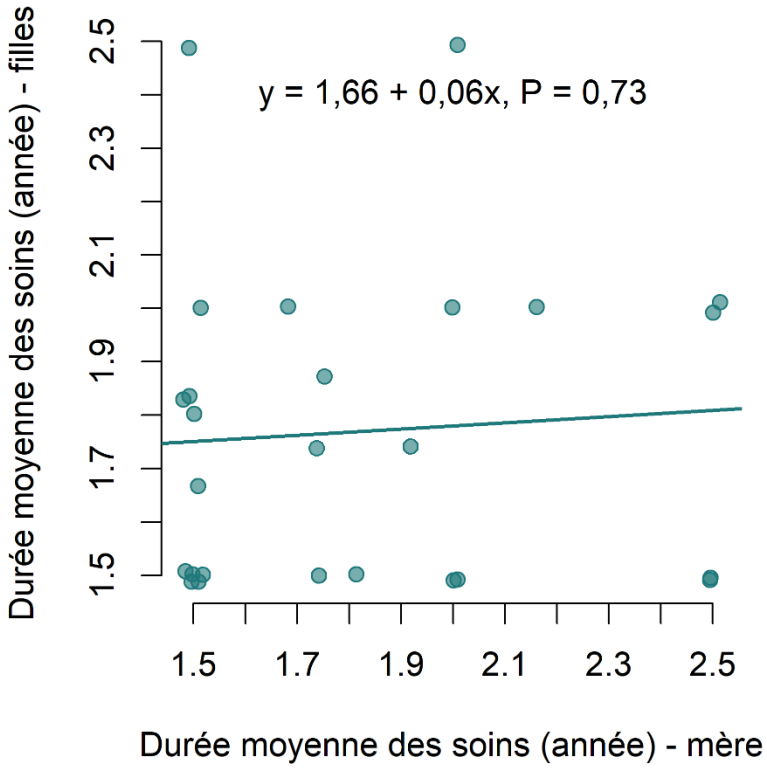

Figure 6.2 **Relation mère-fille pour la durée des soins maternels (valeur de durée moyenne observée au cours du suivi) chez l'ours brun Scandinave (n=26).**

L'équation de la régression est fournie, ainsi que la valeur de P associée au test statistique (modèle linéaire).

6.5 Limites aux observations en milieu naturel

Outre les difficultés associées à la collecte d'échantillons de durées de soins maternels sur un grand nombre d'individus, une limitation importante dans cette étude est l'absence d'observations directes des interactions entre les individus. Chez les ours, on en connaît très

peu sur la lactation. Nos connaissances concernent surtout l'ours polaire ou l'ours brun en captivité, chez qui la lactation atteint un pic à l'été et diminue grandement (Derocher *et al.*, 1993), voire s'arrête (Farley et Robbins, 1995), à la fin de la première année de vie des oursons. Le prélèvement de lait sur l'ours brun scandinave ne fait pas l'objet d'un échantillonnage systématique ou de recherches pour le moment. Toutefois, on tente d'extraire manuellement du lait chez les femelles anesthésiées lors des captures printanières alors que les jeunes sont âgés d'un an et demi. De cette façon, du lait a pu être extrait des mamelles des femelles dans environ 30 % des cas au sud de la Suède (données non publiées), ce qui suggère que l'allaitement peut se prolonger au-delà de la première année, mais nous ne savons pas quand l'allaitement s'est arrêté chez les autres femelles et jusqu'à quand il peut se poursuivre. D'après une étude chez les orangs-outangs, *Pongo* sp., où la lactation s'échelonne sur plusieurs années, il a été suggéré que la prolongation de la lactation pouvait suivre les fluctuations de disponibilité des ressources (Smith *et al.*, 2017). Un tel scénario, où la durée de l'allaitement dépend de la fluctuation de la disponibilité des ressources au printemps, par exemple, serait aussi envisageable chez l'ours brun. De plus, faute d'observations directes et d'échantillons biologiques, nous ne savons pas comment l'importance relative du lait à la diète des oursons change au cours du temps en Scandinavie. L'allaitement débute à la naissance des oursons en plein hiver alors qu'ils sont encore dans leur tanière (Friebe *et al.*, 2014), ce qui rend les observations comportementales logistiquement difficiles. À l'émergence de la tanière, les groupes familiaux comprenant des oursons de l'année ne sont pas capturés pour des raisons éthiques. Il est donc impossible de prélever un échantillon de lait sur les femelles à cette phase importante de la lactation. Bien qu'en Scandinavie les ours adultes soient équipés de colliers VHF/GPS, les femelles adultes occupent un domaine vital large (~124 km^2; Dahle et Swenson, 2003a) et les relocalisations se font principalement par triangulation à partir d'un hélicoptère. Le dérangement occasionné par la présence de l'hélicoptère rend l'observation de comportements naturels questionnable. L'utilisation de colliers équipés de caméras pourrait pallier cette limitation (Hebblewhite et Haydon, 2010). Une autre solution, potentiellement moins coûteuse, serait de récolter les fèces des oursons et d'effectuer des analyses d'isotopes stables pour évaluer la contribution relative du lait et

des autres sources de nourriture à la diète des ours (Bădescu *et al.*, 2017). En consultant les données de localisation des ours, lesquelles sont accessibles aux chercheurs en l'espace de quelques heures en Suède, il est possible d'aller récolter des fèces sur les sites récemment visités par les ours. Récolter ainsi des fèces à intervalle régulier durant toute la période d'association mère-petit permettrait de tester plusieurs hypothèses relatives au patron de changement dans l'importance de la lactation pour les oursons au cours du temps (Figure 6.3). Il serait aussi possible de vérifier l'importance des fluctuations dans les conditions environnementales et de mieux évaluer les coûts associés à des soins maternels longs *vs* courts.

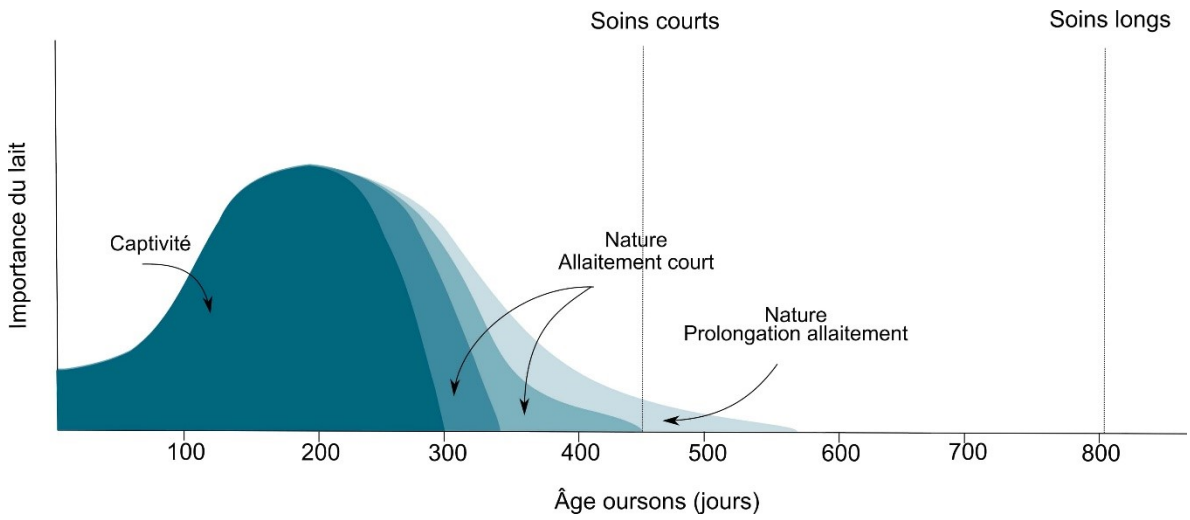

Figure 6.3 Changements hypothétiques dans l'importance du lait pour la diète des oursons de l'ours brun en nature, en comparaison avec les résultats obtenus en captivité (Farley et Robbins, 1995).

En nature, considérant l'accès à la nourriture plus limité, l'allaitement devrait se poursuivre au-delà de l'âge estimé en captivité. Toutefois, l'allaitement pourrait cesser quelque part avant la 2^{e} année de vie des oursons (allaitement court), ou au-delà de la 2^{e} année de vie des oursons (prolongation allaitement), soit pour compenser pour des conditions environnementales plus difficiles ou par « réconfort » (Bădescu *et al.*, 2017).

De façon similaire, le manque d'observations comportementales constitue une limite importante à l'évaluation du rôle des mâles dans la dynamique de séparation des groupes familiaux. À l'aide des données de localisations récoltées aux heures dans le sud de la Suède, il est possible de reconstruire spatialement les interactions entre les ours équipés de colliers GPS et de vérifier qualitativement si des ours mâles étaient présents lors de la séparation des groupes familiaux. Des « colliers-contacts » permettraient aussi de directement détecter les interactions sociales entre les individus (Hebblewhite et Haydon, 2010). Cependant, comme le suivi à long-terme du SBBRP concerne principalement les femelles, la proportion d'ours mâles équipés de colliers GPS est faible. La présence d'autres ours mâles, non équipés, serait donc impossible à écarter.

6.6 Hétérogénéité individuelle au sein des portées

Une supposition du chapitre 2 est que l'hétérogénéité en masse au sein des portées est générée par une allocation maternelle différentielle entre les jeunes. Toutefois, nos analyses reposent sur des mesures prises sur des oursons âgés d'un an et demi. L'alimentation autonome et la compétition intra-fratrie peuvent influencer la masse des jeunes (Sikes, 1998; Gonzalez *et al.*, 2012; Kamel et Williams, 2017) entre le stade ourson de l'année et le stade ourson d'un an. De plus, on sait qu'environ 5 à 20 % des portées sont issues de paternités multiples (Bellemain *et al.*, 2006) et de plus récentes estimations, basées sur le pédigrée de la population de 2016, suggèrent que cette proportion serait plutôt de 45 % (données non publiées). La paternité multiple pourrait être un mécanisme de diversification phénotypique (Jennions et Petrie, 2000) qu'il serait pertinent d'étudier. Néanmoins, il serait important de vérifier si l'hétérogénéité phénotypique des oursons se maintient à l'âge adulte et si celle-ci se traduit en hétérogénéité en valeur adaptative pour déterminer s'il s'agit d'une tactique de reproduction adaptative pour les femelles.

6.7 Conséquences démographiques d'un changement dans la durée des soins maternels

Un changement dans les traits d'histoire de vie et les traits reliés à la reproduction a le potentiel d'influencer la dynamique d'une population (Sinervo *et al.*, 2000; Servanty *et al.*, 2011; Paniw *et al.*, 2018; 2019). Dans une perspective de gestion de la faune, il importe donc de quantifier les conséquences démographiques associées à l'augmentation de la durée des soins maternels dans la population d'ours brun scandinave. Dans le chapitre 5, j'ai estimé quelle serait la valeur de plusieurs paramètres démographiques si la population était constituée de tactiques de reproduction « pures »; c'est-à-dire soit uniquement composée de femelles ayant reçu et prodiguant des soins maternels courts (1,5 ans) ou soit de femelles ayant reçu et prodiguant des soins maternels longs (2,5 ans). J'ai montré que les paramètres démographiques différeraient en absolu, mais surtout en fonction de la pression de chasse. Toutefois, cette approche est biaisée puisque la population réelle n'est pas constituée de tactiques pures, mais plutôt d'un mélange des deux tactiques.

La prochaine étape serait donc de créer un modèle global de dynamique de population femelle-spécifique tenant compte des différentes tactiques de reproduction. Le modèle serait ainsi multi-états (Caswell, 2001) avec des probabilités de transition annuelles (de l'émergence de la tanière au printemps de l'année t à l'émergence de la tanière au printemps de l'année $t+1$) entre les différents états dépendants de la mortalité cause-spécifique (c.-à-d., chasse et naturelle) et de la probabilité de séparation des groupes familiaux. Dans ce modèle (Figure 6.4), 5 stades juvéniles seraient inclus : oursons de l'année, oursons d'un an, oursons de 2 ans dépendants ou indépendants et juvéniles de trois ans. Cette séparation des oursons dépendants et indépendants permet de tenir compte des différences en survie observés chez les oursons d'un an solitaires et ceux accompagnés de leur mère (Van de Walle *et al.*, 2018). Quatre états seraient inclus pour les femelles adultes : solitaire, avec des oursons de l'année, avec des oursons d'un an et avec des

oursons de 2 ans. La plupart des paramètres nécessaires à la paramétrisation du modèle sont déjà disponibles (Bischof *et al.*, 2018); les autres devraient être estimés à partir du suivi longitudinal du SBBRP. À l'aide de ce modèle, il serait possible de quantifier l'effet d'un changement dans un paramètre, telle que la probabilité de séparation des groupes familiaux, sur les processus démographiques, tels que le taux de croissance et le temps de génération. De plus, puisque le modèle intégrerait les taux de mortalité à la chasse pour les différentes classes d'ours, il serait aussi possible de quantifier l'effet des changements dans l'intensité de la chasse et en fonction de différents scénarios de gestion (p. ex. protection légale des femelles uniquement). Développer ce modèle serait donc d'une grande utilité pour la gestion de la population, mais pourrait aussi potentiellement servir à mieux comprendre comment des changements écologiques (ou évolutifs) peuvent avoir des rétroactions sur les processus démographiques.

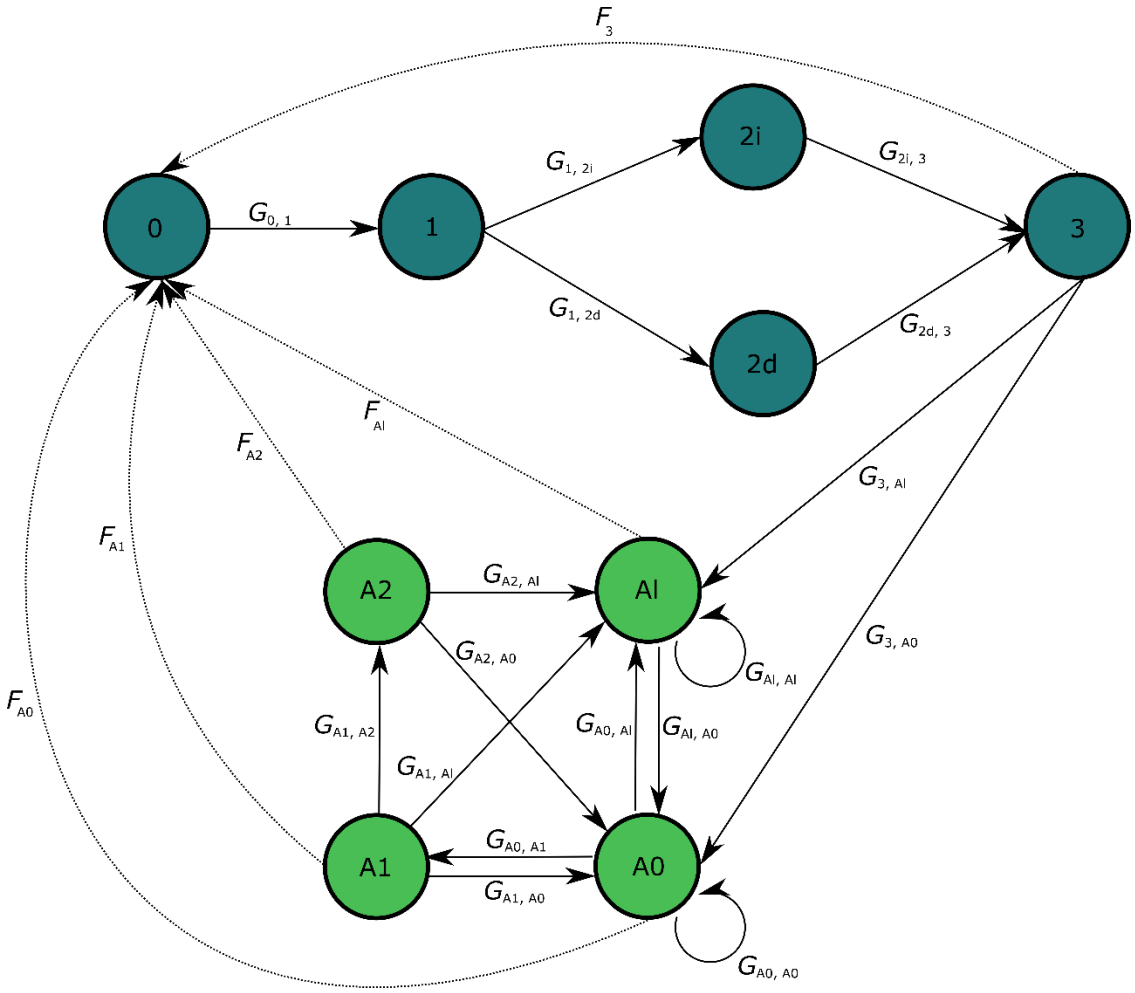

Figure 6.4 **Modèle multi-états femelle-spécifique pour la population d'ours brun dans le sud de la Suède.**

Le modèle inclut 5 classes (âge ou états) pour le stade juvénile (bleu) : oursons de l'année (0), oursons d'un an (1), oursons de deux ans dépendants (2d) et indépendants (2i), et juvéniles de trois ans (3) et 4 classes (états) pour le stade adulte (vert) : solitaire (Al), avec oursons de l'année (A0), avec oursons d'un an (A1), avec oursons de deux ans (A2). D'une année à l'autre, les individus peuvent transiter (flèches pleines) d'une classe d'âge ou d'un état à l'autre selon des probabilités de transition, *G*. Par exemple, la probabilité de transition entre les âges 0 et 1 an ($G_{0,1}$) dépend de la probabilité de survie des oursons de l'année jusqu'à l'année suivante. Les

transitions entre les états adultes incluent aussi des probabilités liées à la reproduction. Par exemple, $G_{3,A0}$ est la probabilité combinée de survie des femelles de 3 ans et de production d'oursons à l'âge de 4 ans. Les flèches pleines et circulaires réfèrent à la probabilité de demeurer dans la même classe l'année suivante (p. ex. les femelles solitaires peuvent demeurer solitaires l'année suivante). Les flèches pointillées représentent la fécondité et réfèrent à la contribution des classes au stade « ourson » via leur survie et la production d'oursons à l'année suivante.

6.8 Conclusion

Pour conclure, ma thèse, utilisant l'ours brun scandinave comme modèle d'étude, s'intéressait à mieux comprendre les causes de variation dans les tactiques de reproduction maternelles et à évaluer les conséquences de cette variation sur la dynamique de la population. Plus précisément, j'ai montré qu'il existe de l'hétérogénéité dans le compromis entre la masse et le nombre de jeunes (chapitre 2), que les causes de variation dans la durée des soins maternels dépendent du contexte (chapitre 3), que les conflits sexuels peuvent affecter la probabilité de prolonger la période de soins maternels (chapitre 4), et que la chasse réglementée peut altérer artificiellement la balance entre coûts et bénéfices des tactiques de reproduction maternelles et affecter les processus démographiques (chapitre 5). On reconnaît l'importance de la variation dans la durée des soins maternels, mais très peu tentent de l'expliquer. À ce titre, ma thèse apporte une contribution inégalée qui, je l'espère, saura inspirer d'autres dans cette voie. Ma thèse a aussi un caractère inusité en ce sens qu'elle rapporte des résultats inattendus, notamment en ce qui concerne la sélection induite par la chasse. En fait, lorsqu'on y réfléchit, une pression de chasse aussi forte que celle observée en Suède est vouée à engendrer de profonds impacts sur la population, nous laissant dubitatifs quant à la pérennité d'une telle pratique. Considérant que les objectifs de gestion de la population sont rarement atteints (Swenson *et al.*, 2017), une pratique avisée pourrait inclure la considération des effets directs et indirects de la chasse dans les plans de gestion.

ANNEXES

7.1 Annexe Chapitre 2

7.1.1 Appendix 2.1: Bear density estimation

We calculated a relative index of local population density for each family group during the yearling year. Annual grids (10 x 10 km cells) of bear density were constructed using two sources of information: 1) county-wide scat-derived DNA collections obtained during organized efforts [1] and 2) annual and country-wide sightings of bears in the fall through the Swedish Large Carnivore Observation Index, LCOI [2]. Data from scat collections were used to produce maps of bear density during the years of scat collection and those maps were corrected for annual trends using the LCOI for the period 1998-2015 [3]. For the periods 1990-1998 and 2015-2016, we assumed a stable density [4] and used the 1998 and 2015 grids, respectively. We used the spatio-temporally explicit maps to derive local population density by extracting a weighted mean of local density within a circular buffer of 7.16 km (average home range radius for an adult female with yearlings [5]) around the median of bear localisations using VHF data prior to 2003 and a combination of VHF and GPS data from 2003 onward. To improve accuracy, we only retained GPS fixes with dilution of precision values <10. We only used relocations during the non-denning period, i.e. between 1 May and 1 November [6].

7.1.2 Appendix 2.2: Classification procedure for yearlings

For each litter of 2 to 4 yearlings, we retained only the lightest and the heaviest yearlings. Sometimes, two or more yearlings had the same mass. In those cases, the relative rank of yearlings was attributed randomly. In singleton litters, resources are not shared among siblings and singletons should receive all energy allocated to reproduction by females. Because of this assumption, singleton litters were included in the analyses to provide a baseline for statistically comparing the mass of those singletons to larger litters. To do so, singletons were randomly classified as "lightest" or "heaviest" in the analyses. Randomisation was performed until the number of "lightest" and "heaviest" yearlings from singleton litters was balanced; i.e. because our sample included 14 such litters, we stopped the procedure when 7 singleton yearlings were randomly classified as "lightest" and 7 as "heaviest".

7.1.3 Appendix 2.3: Supplementary tables and figures

Table A2.1 Observed sex- and litter size-specific mass (kg) of yearling brown bears classified as the "lightest" or "heaviest" in litters from south-central Sweden, 1990-2016.

		Males			Females			All		
Litter size	Yearling rank	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
1	Lightest*	22.0	0.0	3	27.3	7.1	4	25.0	5.7	7
	Heaviest	28.8	7.6	5	21.0	4.2	2	26.5	5.7	7
	All	26.2	6.7	8	25.2	6.6	6	25.8	6.4	14
2	Lightest	19.9	6.2	17	19.5	5.8	37	19.6	5.9	54
	Heaviest	23.3	7.3	34	20.4	5.2	20	22.2	6.7	54
	All	22.2	7.1	51	19.8	5.5	57	20.9	6.4	108
3	Lightest	19.1	5.8	20	17.8	3.9	22	18.4	4.8	42
	Heaviest	23.8	5.8	29	24.3	5.3	13	23.9	5.6	42
	All	21.3	5.8	69	21.0	5.5	59	21.2	5.7	128

*Yearling rank was attributed randomly for singletons.

Table A2.2 Observed litter size-specific sex ratios (proportion of males) among yearling brown bears in south-central Sweden, 1990-2016.

	Mean	SD	*n* (litters)
All yearlings	0.51	0.37	110
Litter size = 1	0.57	0.51	14
Litter size = 2	0.47	0.37	54
Litter size = 3&4	0.53	0.31	42

Table A2.3 Sex-specific composition of brown bear yearling litters in south-central Sweden, 1990-2016.

Sex-specific litter composition	*n* (litters)
M	8
F	6
MM	13
FF	16
MF	25
MMM	6
MMF	16
MFF	12
FFF	6
MMMM	1
MMMF	1
MMFF	0
MFFF	0
FFFF	0

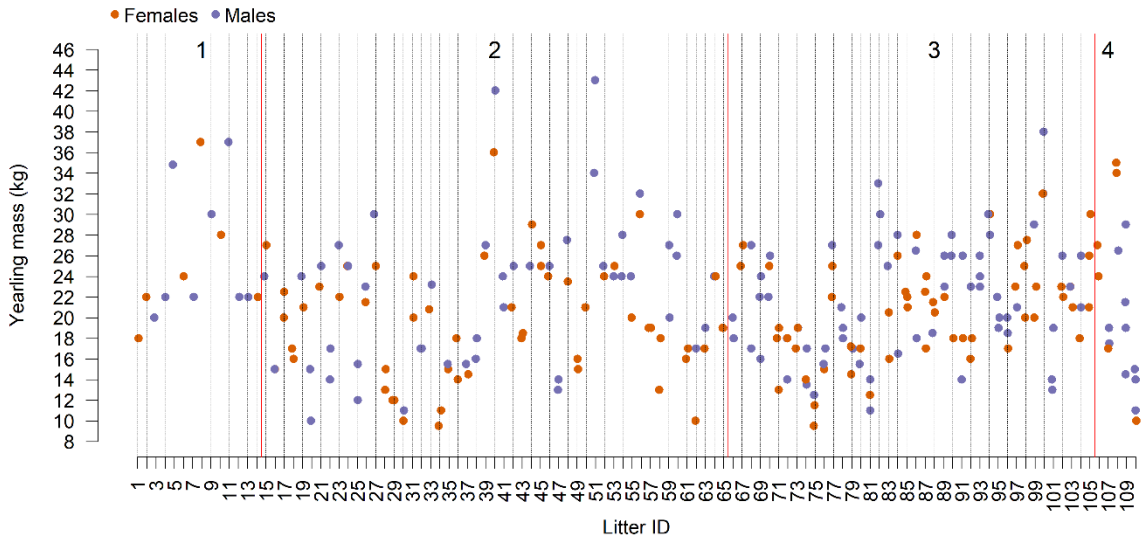

Figure A2.1 Observed sex and litter size-specific distribution of yearling mass in brown bear litters in south-central Sweden, 1990-2016. Litter sizes (1, 2, 3 and 4) are shown on top and are separated by red lines.

7.1.4 Appendix 2.4: Comparison of yearling mass between litters of 2 and 3+ yearlings (no singletons).

We tested whether the trade-off between yearling mass and number was borne differently, i.e., if the slope of the relationship differed, among yearlings from the same litter in litters of 2-3+ yearlings. We retained only the lightest and the heaviest yearlings in the analysis. When two or more yearlings had the same mass, their relative rank was attributed randomly. We used a linear mixed effects model with maternal age, maternal size (head circumference), litter size (continuous), local population density (relative bear density within a circular buffer around annual female home range centres, see text for details), yearling rank (2 levels: "lightest" or "heaviest") and the interaction between litter size and yearling rank as explanatory variables and yearling mass (log-transformed to meet model

assumption of homoscedasticity) as the response variable. Random effects included litter identity nested in maternal identity and year of capture. The starting model included all fixed effects and we obtained the final model by backwards selection using Likelihood ratio tests. Variance Inflation Factors were all < 3.

Table A2.4 Estimates from a linear mixed effects model to test whether the trade-off between offspring mass and number is borne differently among yearlings from the same litter in litters of 2 and 3+ yearlings (no singletons) in brown bears from south-central Sweden, 1990-2016 (n=192 yearlings).

				95% CI	
Variables	β	SE	t-value	Lower	Upper
(b) Yearling mass – Rank effect *(conditional R^2 = 91%, marginal R^2 = 34%)**					
Intercept	0.755	0.389	1.938	0.002	1.517
Litter size	-0.023	0.040	-0.581	-0.101	0.058
Maternal size	0.041	0.007	6.422	0.029	0.054
Local density	-0.276	0.105	-2.628	-0.491	-0.070
Rank (lightest)	-.156	0.067	2.331	0.025	0.288
Litter size × Rank (lightest)	-0.142	0.027	-5.265	-0.195	-0.089
Random effects	Variance	SD			
Litter ID × Maternal ID	0.015	0.121			
Maternal ID	0.006	0.078			
Year	0.033	0.182			
Residual	0.009	0.093			

Variables excluded: Litter size × Maternal size (χ^2=1.760, P = 0.185), Sex (χ^2=0.004, P = 0.949), Sex ratio (χ^2 =0.016, P = 0.890), Maternal age (χ^2 = 2.122, P = 0.145)

*Conditional and marginal coefficients of determination (R2 [7]) were obtained using the R package MuMIn [8].

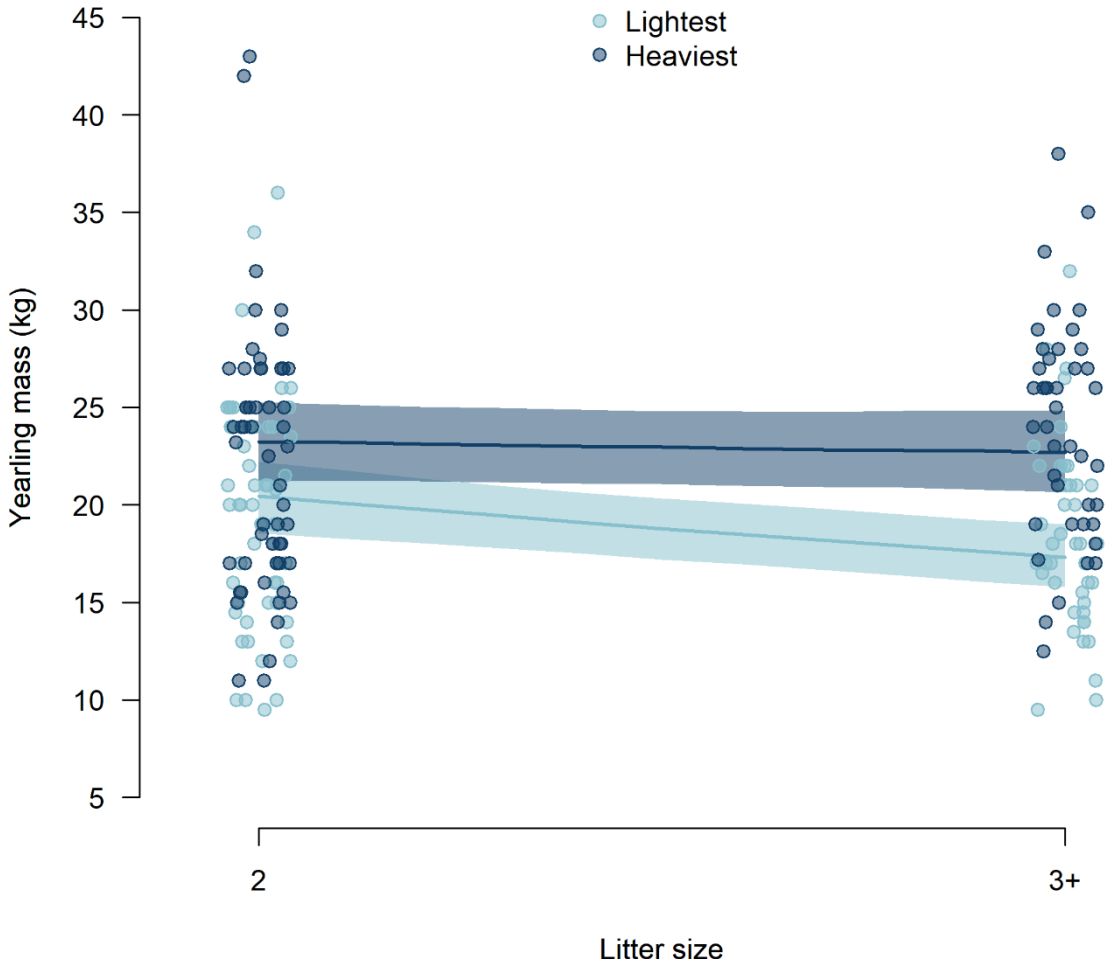

Figure A2.2 Trade-off between offspring mass and number in Scandinavian brown bears, investigated from the perspective of the lightest (light blue) and the heaviest (dark blue) yearling from a litter in litters of 2 and 3+ yearlings (n = 93 litters).

The trade-off (negative relationship) between yearling mass and litter size is strongest when considering only the lightest yearling and disappears when considering only the heaviest yearling. In the figure, observations (circles) and model predictions (solid lines) are back-transformed on the original scale for yearlings from average-size mothers at average local density, along with 95 % confidence intervals (shaded polygons).

7.1.5 References appendix 2

1. Bellemain E, Swenson JE, Tallmon D, Brunberg S, Taberlet P. 2005 Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. *Conserv. Biol.* 19, 150–161. (doi:10.1111/j.1523-1739.2005.00549.x)

2. Kindberg J, Swenson JE, Ericsson G, Bellemain E, Miquel C, Taberlet P. 2011 Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biol.* 17, 114–123. (doi:10.2981/10-100)

3. Leclerc M, Frank SC, Zedrosser A, Swenson JE, Pelletier F. 2017 Hunting promotes spatial reorganization and sexually selected infanticide. *Sci. Rep.* 7, 45222. (doi:10.1038/srep45222)

4. Swenson JE, Schneider M, Zedrosser A, Söderberg A, Franzén R, Kindberg J. 2017 Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. *Wildlife Biol.*, doi:10.2981/wlb.00251.

5. Dahle B, Swenson JE. 2003 Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos. J. Anim. Ecol.* 72, 660–667. (doi:10.1046/j.1365-2656.2003.00737.x)

6. Friebe A, Swenson JE, Sandegren F. 2001 Denning chronology of female brown bears in central Sweden. *Ursus* 12, 37–45.

7. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x)

8. Barton K. 2009 MuMIn: Multi-model inference. R package version 1.40.0. https://cran.r-project.org/package=MuMIn.

7.2 Annexe Chapitre 3

7.2.1 Appendix 3.1: Correlation plots between explanatory variables included as potential determinants of the duration of maternal care

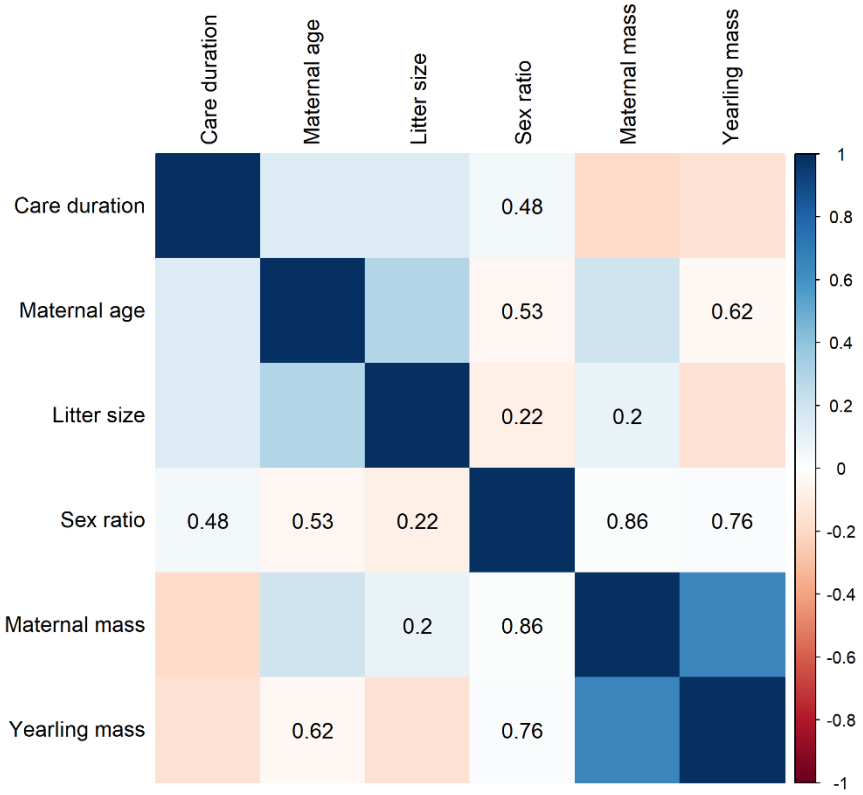

Figure A3.1 Correlation plot between numeric variables included in the candidate models to identify the determinants of the duration of brown bear maternal care in both populations (North and South) in Sweden, 1990-2019.

Sex ratio represents the proportion of males within a litter. Correlations range from strongly negative (-1 = dark red) to strongly positive (+1 = dark blue). When non-significant, p-values associated with the correlation tests are given.

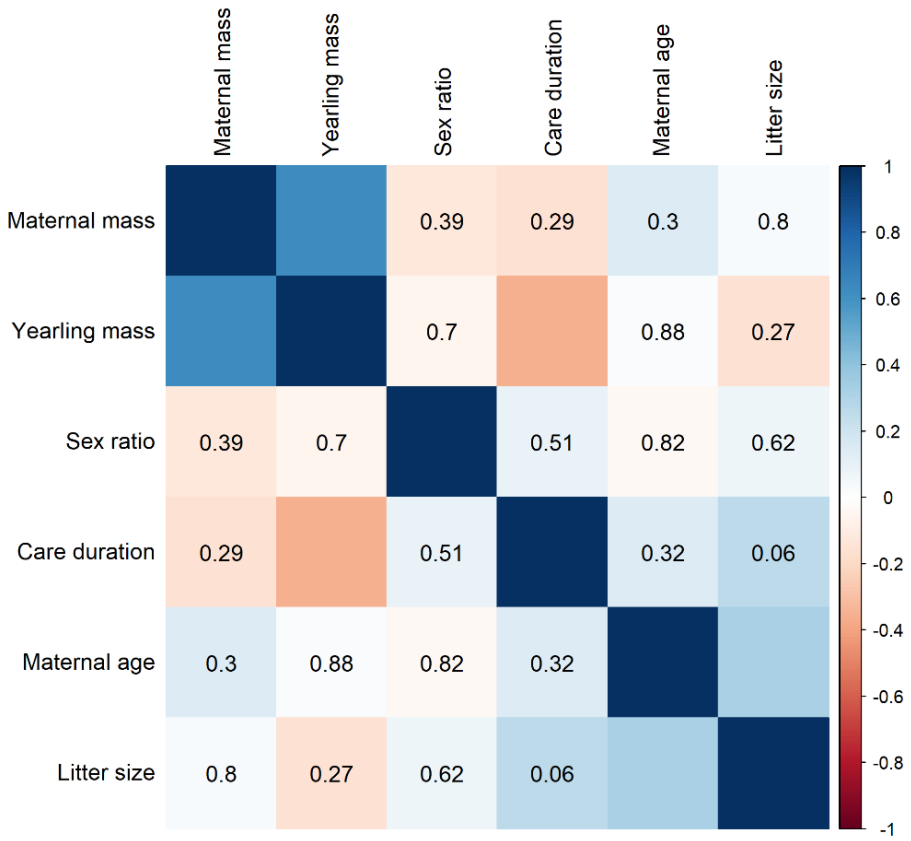

Figure A3.2 Correlation plot between numeric variables included in the candidate models to identify the determinants of the duration of brown bear maternal care in northern Sweden, 1993-2011.

Sex ratio represents the proportion of males within a litter. Correlations range from strongly negative (-1 = dark red) to strongly positive (+1 = dark blue). When non-significant, p-values associated with the correlation tests are given.

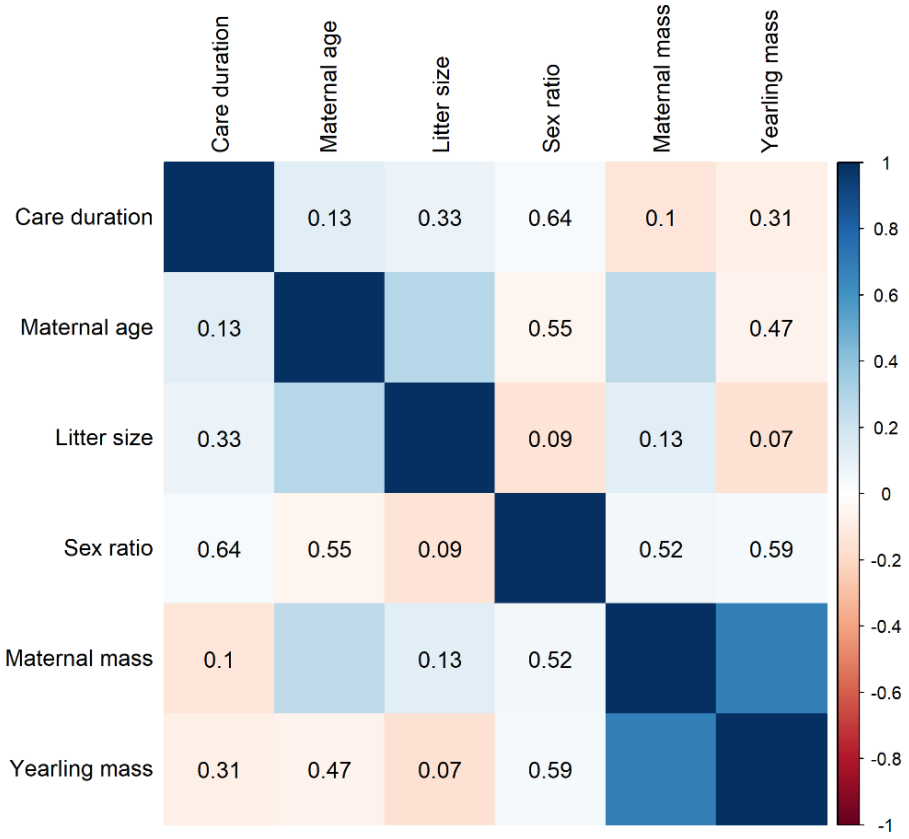

Figure A3.3 Correlation plot between numeric variables included in the candidate models to identify the determinants of the duration of brown bear maternal care in southern Sweden, 1990-2019.

Sex ratio represents the proportion of males within a litter. Correlations range from strongly negative (-1 = dark red) to strongly positive (+1 = dark blue). When non-significant, p-values associated with the correlation tests are given.

7.2.2 Appendix 3.2: Supplementary Table A3.1

Table A3.1 Path coefficients from the best performing hypothetical causal structure linking maternal and litter characteristics to the duration of maternal care in Scandinavian brown bears from (a) two populations (North, South) in Sweden from 1990-2019, (b) the North population from 1993-2011, and (c) the South population from 1990-2019.

Response variable	Explanatory variable	Estimate	SE	P
(a) Both populations				
Maternal mass	Intercept	-0.087	0.094	0.352
	Maternal age	**0.130**	**0.061**	**0.034**
Yearling mass	Intercept	0.639	0.158	<0.001
	Maternal mass	**0.742**	**0.053**	**<0.001**
	Litter size	**-0.303**	**0.069**	**<0.001**
	Maternal age	**-0.158**	**0.052**	**0.003**
Duration of maternal care	Intercept	-2.642	0.894	0.003
	Litter size	**0.818**	**0.367**	**0.026**
	Maternal age	**0.481**	**0.231**	**0.038**
	Maternal mass	**-0.579**	**0.246**	**0.019**
Litter size	Intercept	0.745	0.048	<0.001
	Maternal age	**0.092**	**0.046**	**0.045**
(b) North population				
Maternal mass	Intercept	-0.325	0.167	0.065
	Maternal age	0.021	0.125	0.866
Yearling mass	Intercept	0.884	0.328	0.013
	Maternal mass	**0.677**	**0.104**	**<0.001**
	Litter size	-0.292	0.146	0.058
	Maternal age	-0.051	0.101	0.618
Duration of maternal care	Intercept	0.518	0.433	0.232
	Yearling mass	**-1.180**	**0.557**	**0.034**

Table A3.1 (Continued)

(c) South population				
Maternal mass	Intercept	0.040	0.110	0.722
	Maternal age	**0.200**	**0.068**	**0.005**
Yearling mass	Intercept	0.535	0.173	0.003
	Maternal mass	**0.791**	**0.061**	**<0.001**
	Litter size	**-0.314**	**0.074**	**<0.001**
	Maternal age	**-0.196**	**0.057**	**<0.001**
Duration of maternal care	Intercept	-3.035	1.239	0.014
	Litter size	0.700	0.468	0.135
	Maternal age	**0.572**	**0.290**	**0.049**
	Maternal mass	-0.431	0.332	0.194
Litter size	Intercept	0.745	0.056	<0.001
	Maternal age	0.091	0.056	0.105

Statistically significant values are given in bold. Coefficients are presented on the transformed scaled for care duration (logit) and litter size (log).

7.2.3 Appendix 3.3: Path analysis for the South including local population density, 1990-2019

For each family group, we calculated an index of local population density during the year of capture. To do so, we combined three sources of information: 1) DNA sampling, 2) reported sightings of bears and 3) telemetry-derived bear localisations. DNA sampling through scat collection takes place during organized efforts at the county level approximately every ten years (Bellemain, Swenson, Tallmon, Brunberg, & Taberlet, 2005). DNA analysis allows determining the number of distinct bears in a given area. With this information, maps of bear density (10 x 10 km cells) were produced during the years of scat collection (Frank et al., 2018). Those maps were corrected for annual trends using annual and country-wide sightings of bears in the fall through the Swedish Large Carnivore

Observation Index, LCOI (Kindberg et al., 2011), which resulted in annual grids of bear density throughout Sweden. The LCOI is available from 1998-2015. For the periods 1990-1998 and 2015-2019, we assumed a stable density (Swenson et al., 2017) and used the 1998 and 2015 grids, respectively. Then, we used telemetry data on individual bears to derive an index of local population density. For each family group, we extracted VHF data (prior to 2003) and a combination of VHF and GPS data (from 2003 onward) from collared mothers during the year of capture to construct a circular buffer of 7.16 km (average home range radius for an adult female with yearlings; Dahle and Swenson 2003) around the median of bear localisations. Then, we used the spatio-temporally explicit maps to derive local population density by extracting a weighted mean of local density within the buffer. To improve accuracy, we only retained GPS fixes with dilution of precision values <10. We only used relocations during the non-denning period, i.e. between 1 May and 1 November (Friebe, Swenson, & Sandegren, 2001). Our dataset comprised 141 litters for the variable selection procedure and 152 litters for the path analyses.

We used the same model selection procedure as in the main text to verify whether the duration of maternal care was correlated with bear density, but we added a model containing the variable "density" in the candidate models set. All models (GLMM) included maternal identity as a random factor. Despite being highly correlated with both yearling and maternal mass (Figure A3.4), bear density did not seem to be important in explaining the duration of maternal care in brown bears as the model including the variable did not perform better than the null model (Table A3.2). Then, we added the variable "density" in the causal hypothesis #7 (the best causal structure explaining variation in the duration of maternal care in the South) with direct links with maternal mass, yearling mass and the duration of maternal care (Figure A3.5a). We also added a direct link between density and maternal age to account for potential density effects on age. structure. The *C* statistic from the d-separation claims for the causal structure was 2.13 (P = 0.91) and was thus not rejected. Results are presented in Table A3.3 and on Figure A3.5b.

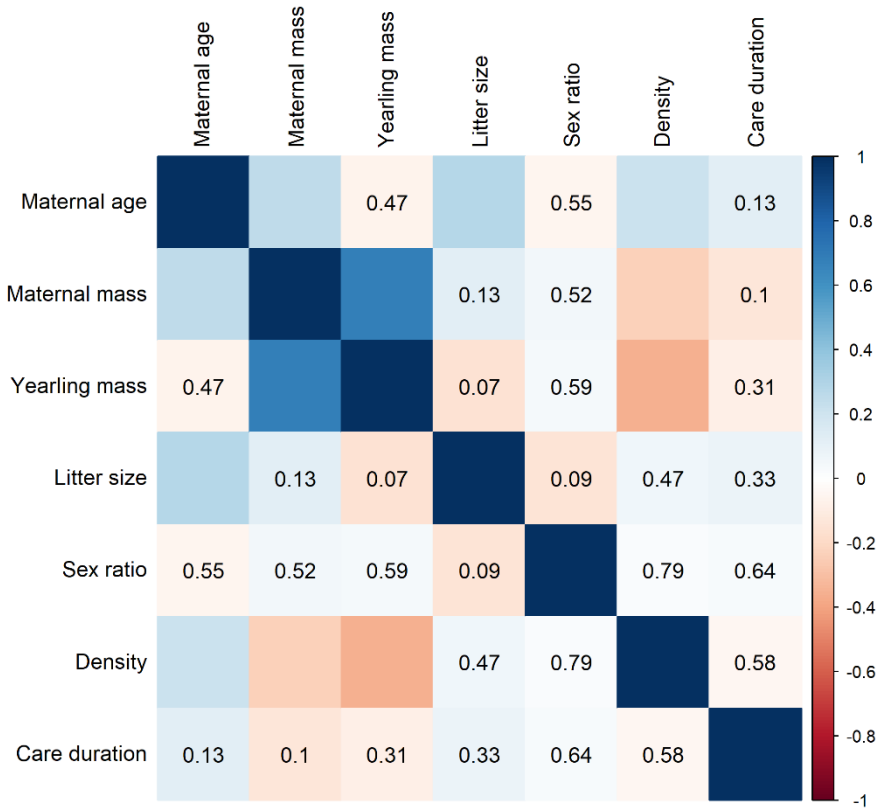

Figure A3.4 Correlation plot between numeric variables included in the candidate models to identify the determinants of the duration of brown bear maternal care in the southern population in Sweden, 1990-2019.

Sex ratio represents the proportion of males within a litter. Correlations range from strongly negative (-1 = dark red) to strongly positive (+1 = dark blue). When non-significant, p-values associated with the correlation tests are given.

Table A3.2 Candidate generalized mixed effects models constructed to determine variables affecting the duration of maternal care (response variable) in Scandinavian brown bears from the south population from 1990-2019.

Model	K	ΔAICc	$AICc_w$
Litter size	**3**	**0.00**	**0.27**
Maternal age	**3**	**1.12**	**0.15**
Litter size + Sex ratio	**4**	**1.45**	**0.13**
Null	2	2.19	0.09
Maternal age + Reproductive status	4	3.21	0.05
Maternal mass	3	3.47	0.05
Yearling mass + Litter size + Sex ratio	5	3.58	0.05
Maternal mass + Maternal age + Reproductive status	5	3.62	0.04
Yearling mass	3	3.85	0.04
Density	3	3.96	0.04
Reproductive status	3	3.97	0.04
Sex ratio	3	4.07	0.04
Maternal mass + Maternal age + Reproductive status + Yearling mass + Litter size + Sex ratio	9	5.76	0.02

All models included maternal identity as random intercept. Are presented in the table for each model: the number of parameters (K), the difference in AIC value corrected for small sample with the best performing model (ΔAICc), and model weight ($AICc_w$). In bold are models within 2 AICc of the best performing model.

Table A3.3 Path coefficients from the best performing hypothetical causal structure linking maternal traits, yearling mass, and litter size to the duration of maternal care in Scandinavian brown bears from the south population from 1990-2019.

Response variable	Explanatory variable	Estimate	SE	P
Maternal mass	Intercept	-0.069	0.106	0.516
	Maternal age	**0.262**	**0.067**	**<0.001**
	Density	**-0.385**	**0.104**	**<0.001**
Yearling mass	Intercept	0.650	0.173	<0.001
	Maternal mass	**0.757**	**0.063**	**<0.001**
	Litter size	**-0.317**	**0.075**	**<0.001**
	Maternal age	**-0.168**	**0.058**	**0.004**
	Density	-0.103	0.075	0.171
Maternal age	Intercept	-0.106	0.097	0.274
	Density	**0.257**	**0.096**	**0.009**
Duration of maternal care	Intercept	1.388	2.704	0.608
	Litter size	0.651	0.452	0.150
	Maternal age	**0.668**	**0.287**	**0.020**
	Maternal mass	-0.049	0.027	0.074
	Density	-0.551	0.353	0.118
Litter size	Intercept	0.741	0.056	<0.001
	Maternal age	0.088	0.054	0.105

Statistically significant values are shown in bold. Coefficients are presented on the transformed scaled for care duration (logit) and litter size (log).

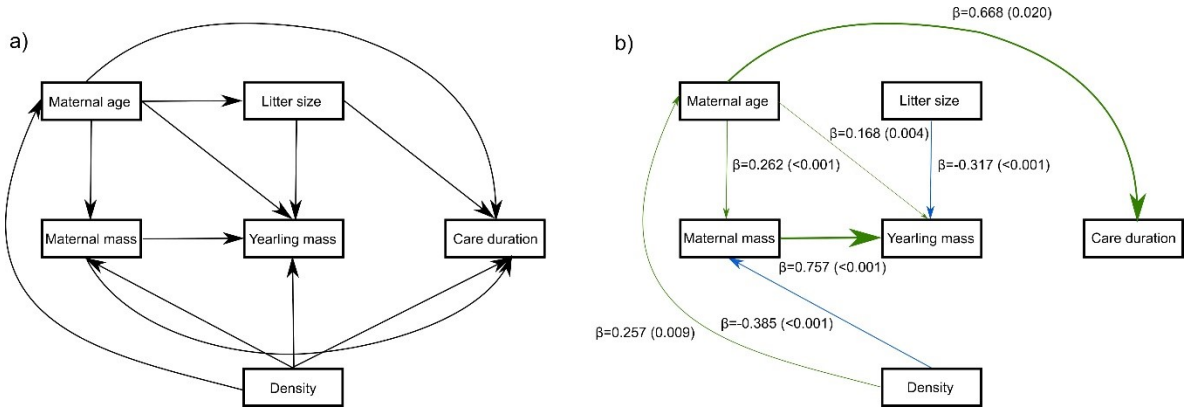

Figure A3.5 Hypothetical (a) and simplified (b) causal structure to explain variation in the duration of maternal care in Scandinavian brown bears from the South population from 1990-2019.

The causal structure included hypothetical direct contributions of local density. Path coefficients are presented along with their associated p-values in parenthesis. Only significant relationships are shown. Positive relationships are represented by solid green arrows, whereas negative relationships are presented by dashed blue arrows. Arrows width is proportional to effect size. Coefficients are presented on the transformed scaled for care duration (logit) and litter size (log).

7.2.4 Appendix 3.4: Path analysis for the South including berry abundance, 2007-2016

Berries are among the most important food items for brown bears in Sweden, especially as they are found in high abundance in the fall, prior to bear hibernation (Stenset et al., 2016). Before entering the den, bears accumulate fat reserves by eating berries in large quantities during a period called hyperphagia. In southern Sweden, fluctuations in berry abundance in the autumn has been linked with changes in both maternal and yearling mass in the spring (Hertel et al., 2018). Therefore, as it correlates with yearling mass, berry abundance could also correlate with the duration of maternal care. Moreover, according to the *timing hypothesis* presented in (Balme, Robinson, Pitman, & Hunter, 2017), females could extend the period of maternal care in periods of lower food abundance to ensure cubs are weaned at a favorable time. Therefore, females might decide to continue or terminate the duration of maternal care based on berry abundance independently of its effect on yearling mass. However, due to the extensive effort required to monitor fluctuations in berry abundance over time, it was only possible to derive an annual index of berry abundance for the period 2006-2015 (i.e. 10 years) in southern Sweden. See Hertel et al. (2018) for more information on how annual index of berry was calculated. We focused on the abundance of bilberry (*Vaccinium myrtillus*), as it is the most important berry species for bears in the southern population (Stenset et al., 2016), and we used berry abundance in the fall previous to bear captures in the spring. Limiting our dataset to 2007-2016 in the southern population, our dataset comprised 57 litters for the variable selection procedure and 59 litters for the path analyses.

We used the same model selection procedure as in the main text to verify whether the duration of maternal care was correlated with berry abundance, but we added a model containing the variable “berry index” in the candidate models set. Due to convergence issues using GLMM with a reduced sample size, we relied on GLM (maternal identity was removed as random effect) instead. Despite being highly correlated with both yearling and

maternal mass (Figure A3.6), berry abundance did not seem to be important in explaining the duration of maternal care in brown bears as the model including the variable did not perform better than the null model (Table A3.4). Then, we added the variable "berry" in the causal hypothesis #7 (the best causal structure explaining variation in the duration of maternal care in the South) with direct links with maternal mass, yearling mass and the duration of maternal care (Figure A3.7a). The *C* statistic from the d-separation claims for the causal structure was 11.07 (P = 0.20) and was thus not rejected. Results are presented in Table A3.5 and on Figure A3.7b.

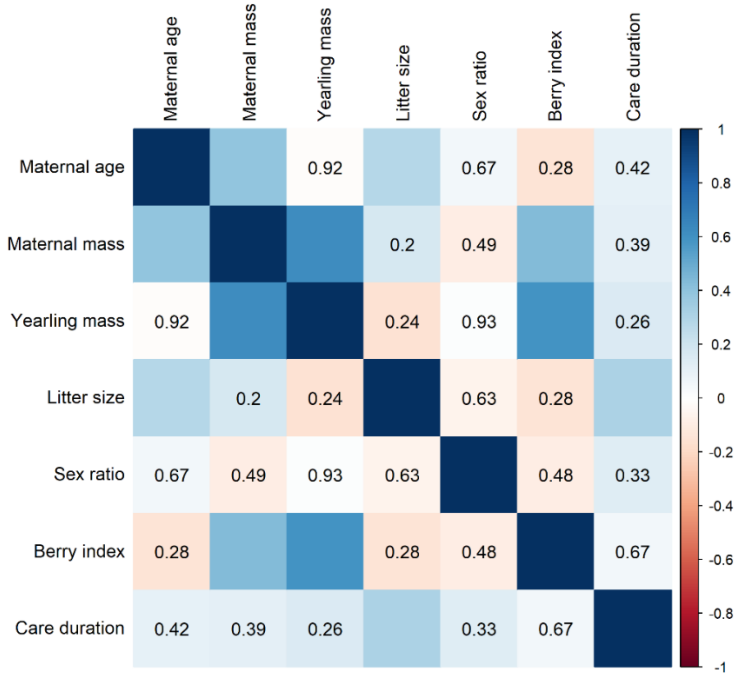

Figure A3.6 Correlation plot between numeric variables included in the candidate models to identify the determinants of the duration of brown bear maternal care in the southern population in Sweden, 2006-2015, when an index of berry abundance could be derived (n = 57 litters).

Sex ratio represents the proportion of males within a litter. Correlations range from strongly negative (-1 = dark red) to strongly positive (+1 = dark blue). When non-significant, p-values associated with the correlation tests are given.

Table A3.4 Candidate generalized linear models constructed to determine variables affecting the duration of maternal care (response variable) in Scandinavian brown bears from the South population from 2007-2016, when an index of berry abundance was calculated (n = 57 litters).

Model	K	ΔAICc	$AICc_w$
Yearling mass + Litter size + Sex ratio	**4**	**0.00**	**0.32**
Litter size	**2**	**0.20**	**0.29**
Litter size + Sex ratio	**3**	**0.93**	**0.20**
Null	1	3.91	0.05
Yearling mass	2	4.72	0.03
Sex ratio	2	5.09	0.02
Maternal mass	2	5.27	0.02
Maternal age	2	5.38	0.02
Reproductive status Reproductive status	2	5.61	0.02
Berry index	2	5.86	0.02
Maternal age + Reproductive status	3	7.44	0.01
Maternal mass + Maternal age + Repr	4	9.39	0.00
Maternal mass + Maternal age + Reproductive status + Yearling mass + Litter size + Sex ratio	8	9.66	0.00

Are presented in the table for each model: the number of parameters (K), the difference in AIC value corrected for small sample with the best performing model (ΔAICc), and model weight ($AICc_w$). In bold are models within 2 AICc of the best performing model.

Table A3.5 Path coefficients from the best performing hypothetical causal structure linking maternal traits, yearling mass and litter size to the duration of maternal care in Scandinavian brown bears from the southern population from 2007-2016, when an index of berry production was calculated (n = 59 litters).

Response variable	Explanatory variable	Estimate	SE	P
Maternal mass	Intercept	0.000	0.10	1.00
	Maternal age	**0.510**	**0.107**	**<0.001**
	Berry index	**0.456**	**0.107**	**<0.001**
Yearling mass	Intercept	0.699	0.303	0.025
	Maternal mass	**0.662**	**0.114**	**<0.001**
	Litter size	**-0.338**	**0.140**	**0.019**
	Maternal age	-0.142	0.110	0.201
	Berry index	**0.213**	**0.106**	**0.049**
Duration of maternal care	Intercept	-2.376	1.026	0.021
	Litter size	**0.947**	**0.463**	**0.041**
	Maternal age	0.114	0.336	0.734
	Maternal mass	-0050	0.351	0.887
	Berry index	0.241	0.341	0.481
Litter size	Intercept	0.723	0.091	<0.001
	Maternal age	0.078	0.088	0.377

Statistically significant values are shown in bold. Coefficients are presented on the transformed scaled for care duration (logit) and litter size (log).

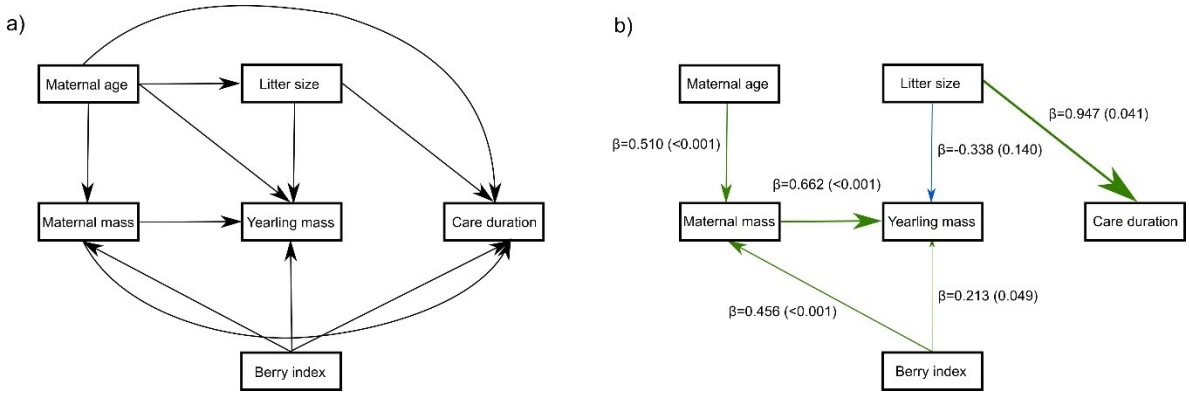

Figure A3.7 Hypothetical (a) and simplified (b) causal structure to explain variation in the duration of maternal care in Scandinavian brown bears from the South population from 2007-2016.

The causal structure included hypothetical direct contributions of berry abundance in the previous fall. Path coefficients are presented along with their associated p-values in parenthesis. Only significant relationships are shown. Positive relationships are represented by solid green arrows, whereas negative relationships are presented by dashed blue arrows. Arrows width is proportional to effect size. Coefficients are presented on the transformed scaled for care duration (logit) and litter size (log).

7.2.5 References appendix 3

Balme, G. A., Robinson, H. S., Pitman, R. T., & Hunter, L. T. B. (2017). Flexibility in the duration of parental care: female leopards prioritise cub survival over reproductive output. *Journal of Animal Ecology*, *86*(5), 1224–1234. doi: 10.1111/1365-2656.12713

Bellemain, E., Swenson, J. E., Tallmon, D., Brunberg, S., & Taberlet, P. (2005). Estimating population size of elusive animals with DNA from hunter-collected feces: four

methods for brown bears. *Conservation Biology, 19*(1), 150–161. doi: 10.1111/j.1523-1739.2005.00549.x

Dahle, B., & Swenson, J. E. (2003). Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology, 72*(4), 660–667. doi: 10.1046/j.1365-2656.2003.00737.x

Frank, S. C., Leclerc, M., Pelletier, F., Rosell, F., Swenson, J. E., Bischof, R., … Zedrosser, A. (2018). Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. *Journal of Animal Ecology, 87*, 247–258.

Friebe, A., Swenson, J. E., & Sandegren, F. (2001). Denning chronology of female brown bears in central Sweden. *Ursus, 12*, 37–46.

Hertel, A. G., Bischof, R., Langval, O., Mysterud, A., Kindberg, J., Swenson, J. E., & Zedrosser, A. (2018). Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos, 127*(2), 197–207. doi: 10.1111/oik.04515

Kindberg, J., Swenson, J. E., Ericsson, G., Bellemain, E., Miquel, C., & Taberlet, P. (2011). Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology, 17*(2), 114–123. doi: 10.2981/10-100

Stenset, N. E., Lutnæs, P. N., Bjarnadóttir, V., Dahle, B., Fossum, K. H., Jigsved, P., … Swenson, J. E. (2016). Seasonal and annual variation in the diet of brown bears *Ursus arctos* in the boreal forest of southcentral Sweden. *Wildlife Biology, 22*(3), 107–116. doi: 10.2981/wlb.00194

Swenson, J. E., Schneider, M., Zedrosser, A., Söderberg, A., Franzén, R., & Kindberg, J. (2017). Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. Wildlife Biology, wlb.00251. doi: 10.2981/wlb.00251

7.3 Annexe Chapitre 4

7.3.1 Appendix 4.1: Supporting tables and figures

Table A4.1 Summary characteristics for brown bears within each group considered in the analyses.

ID	Start date	End date	Group	Age	No. relocations
B_3	2007-04-16	2007-06-29	Male	16	3040
B_3	2008-04-28	2008-07-11	Male	17	3272
B_7	2008-04-20	2008-05-27	Male	10	1694
B_8	2003-04-17	2003-06-08	Male	5	2206
B_14	2008-04-13	2008-05-17	Male	5	1614
B_14	2009-04-12	2009-06-13	Male	6	1536
B_14	2010-04-15	2010-07-05	Male	7	3782
B_14	2011-04-18	2011-05-27	Male	8	1892
B_14	2012-04-01	2012-05-21	Male	9	1584
B_14	2014-04-26	2014-05-14	Male	11	796
B_16	2008-04-19	2008-06-02	Male	8	2100
B_16	2010-04-11	2010-05-19	Male	10	1722
B_16	2011-04-10	2011-05-05	Male	11	1082
B_17	2008-04-20	2008-05-15	Male	6	924
B_17	2010-04-15	2010-06-22	Male	8	2382
B_17	2012-04-01	2012-05-22	Male	10	1292
B_17	2013-04-21	2013-06-12	Male	11	2306
B_17	2014-04-18	2014-05-09	Male	12	1030
B_19	2008-04-16	2008-07-15	Male	5	2674
B_19	2010-04-17	2010-05-19	Male	7	1544
B_19	2011-04-11	2011-06-19	Male	8	3144
B_20	2008-04-18	2008-05-30	Male	16	1896
B_21	2008-04-19	2008-07-05	Male	6	2940
B_21	2010-04-29	2010-05-23	Male	8	1116

Table A4.1 (Continued)

B_21	2011-04-01	2011-07-07	Male	9	4474
B_21	2012-04-01	2012-06-30	Male	10	2948
B_21	2013-06-02	2013-07-09	Male	11	1786
B_22	2012-04-09	2012-06-13	Male	5	2468
B_22	2013-04-13	2013-05-22	Male	6	1752
B_23	2012-04-01	2012-05-12	Male	5	1798
B_23	2013-04-19	2013-05-22	Male	6	1604
B_25	2009-04-15	2009-07-05	Male	5	3668
B_25	2010-04-15	2010-06-28	Male	6	3338
B_26	2009-05-17	2009-07-01	Male	7	2062
B_27	2009-05-17	2009-06-15	Male	6	1384
B_28	2010-04-16	2010-06-27	Male	10	3354
B_28	2011-04-12	2011-05-24	Male	11	1834
B_29	2011-04-03	2011-05-10	Male	7	1408
B_29	2012-04-01	2012-05-11	Male	8	1050
B_30	2010-05-31	2010-06-12	Male	6	272
B_30	2011-04-10	2011-05-12	Male	7	1216
B_31	2013-04-20	2013-06-09	Male	5	262
B_32	2013-04-23	2013-05-03	Male	13	492
B_32	2014-04-01	2014-07-11	Male	14	4140
B_32	2015-04-01	2015-06-24	Male	15	3854
B_32	2016-04-05	2016-07-09	Male	16	3126
B_33	2014-04-19	2014-06-01	Male	6	2072
B_34	2015-04-06	2015-06-15	Male	6	3056
B_35	2013-06-02	2013-06-28	Male	6	1236
B_37	2008-04-11	2008-06-03	Male	19	2472
B_37	2009-04-09	2009-05-31	Male	20	1468
B_37	2010-04-23	2010-06-24	Male	21	2898
B_1	2008-05-01	2008-05-29	Long-care female	14	1378
B_4	2009-04-22	2009-07-09	Long-care female	9	1920
B_4	2012-05-05	2012-05-23	Long-care female	12	578
B_4	2015-04-27	2015-05-17	Long-care female	15	668
B_6	2013-05-18	2013-05-29	Long-care female	12	570
B_12	2013-04-26	2013-05-27	Long-care female	8	1318
B_13	2014-04-17	2014-06-30	Long-care female	9	3426
B_18	2010-04-27	2010-05-13	Long-care female	10	814

Table A4.1 (Continued)

B_18	2014-05-01	2014-06-05	Long-care female	14	1724
B_24	2010-05-06	2010-05-22	Long-care female	13	804
B_38	2006-05-06	2006-06-21	Long-care female	13	1890
B_38	2009-04-29	2009-05-21	Long-care female	16	1092
B_1	2004-04-19	2004-07-15	Short-care female	10	3258
B_2	2008-05-03	2008-05-08	Short-care female	9	284
B_5	2007-04-19	2007-06-18	Short-care female	6	2850
B_6	2011-04-28	2011-07-13	Short-care female	10	3590
B_9	2011-04-29	2011-07-13	Short-care female	18	3550
B_10	2006-05-01	2006-05-06	Short-care female	6	272
B_10	2011-05-04	2011-05-19	Short-care female	11	758
B_10	2013-05-25	2013-06-04	Short-care female	13	518
B_11	2011-05-08	2011-05-26	Short-care female	10	624
B_13	2012-04-27	2012-05-03	Short-care female	7	282
B_15	2012-05-05	2012-05-21	Short-care female	11	798
B_15	2014-04-30	2014-05-19	Short-care female	13	944
B_36	2008-05-03	2008-05-08	Short-care female	18	280
B_39	2007-04-22	2007-06-20	Short-care female	11	2790

Start and end dates refer to the period during which GPS data were collected for each bear-year. Start date corresponds to den emergence, i.e. the first date when available GPS data showed movements away from the denning site. For short-care females, end date corresponds to actual family break-up date. For males and long-care females, it corresponds to a fictive date of family break-up randomly drawn from the density distribution of family break-ups obtained for short-care females. No. relocations corresponds to the total number of geographic localisations used in the analyses (half corresponds to actual GPS relocations, i.e. resource use, and the other half to randomly drawn locations within the bear annual home range, i.e. resource availability).

Table A4.2 Model-based predictions of selection coefficients for Scandinavian brown bear adult males, short-care females and long-care females in south-central Sweden, 2004-2016

	Males			Short-care females			Long-care females		
		95% CI			95% CI			95% CI	
Variable	Selection coefficient	Lower	Upper	Selection coefficient	Lower	Upper	Selection coefficient	Lower	Upper
Road	0.05	0.04	0.07	-0.07	-0.10	-0.04	0.09	0.05	0.13
Habitation	-0.09	-0.11	-0.08	0.07	0.04	0.10	0.43	0.39	0.47
Old_Forest	-0.23	-0.26	-0.20	-0.17	-0.26	-0.09	-0.14	-0.23	-0.04
Mid_Aged_Forest	-0.18	-0.21	-0.15	-0.10	-0.18	-0.02	-0.37	-0.46	-0.29
Bog	-0.56	-0.60	-0.51	-0.56	-0.67	-0.46	-1.00	-1.14	-0.86
Clearcut	-0.33	-0.39	-0.27	0.24	0.08	0.40	0.01	-0.16	0.17

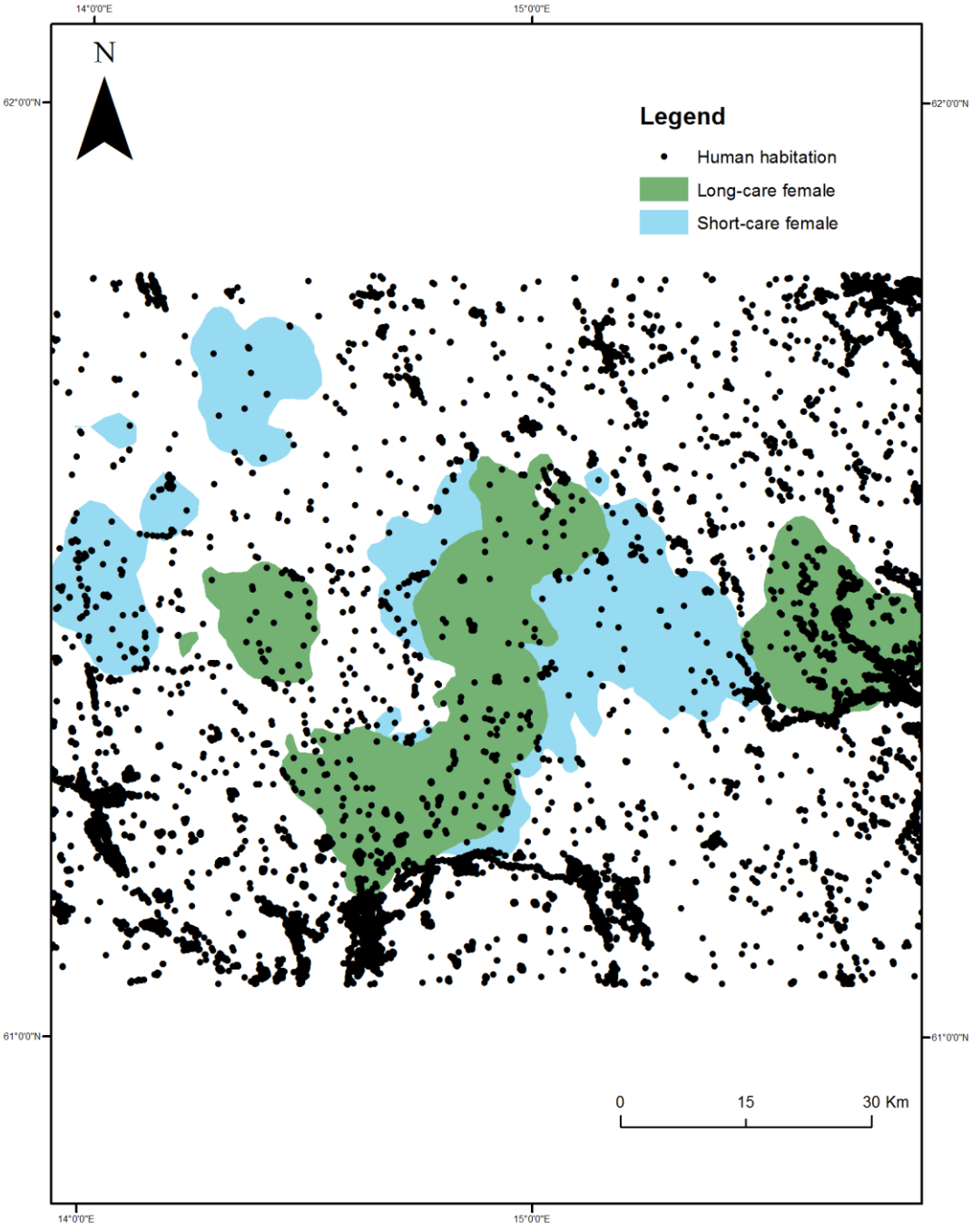

Figure A4.1 **Distribution of human habitations in the study area (black dots) along with the home range of short- (blue areas) and long- (green areas) care female brown bears in southcentral Sweden.**

7.3.2 Appendix 4.2: Intra-individual comparison of habitat selection patterns

We compared habitat selection during the mating season of individual females (n=4) from the year they were with yearlings (time *t*; the year when the female kept the yearlings) to the year they were with 2-year-olds (time *t*+1; the year of mother-offspring separation). We had sufficient GPS data from den emergence until a randomly assigned date of family break-up (time *t*) and the date of actual family break-up (time *t+1*) for only four females. We used RSFs with the same fixed and random effect structure as described in the methods section, but this time "group" was set as a 2-levels factor ("keeping female" and "female with 2-year-olds") in interaction with all land cover types and human distances variables.

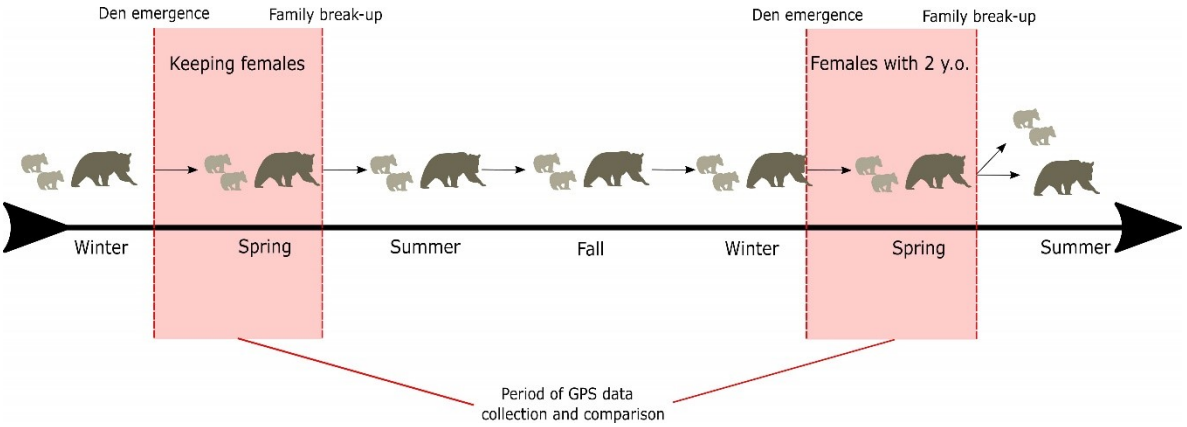

Figure A4.2 Timeline showing that GPS data used to make intra-individual comparisons of habitat selection patterns were collected between den emergence and the period of family break-up when females were accompanied by dependent yearlings and dependent 2 year-olds.

Table A4.3 **Parameter estimates (β) from logistic regression to evaluate resource selection of brown bear females (n=4) between the year they were accompanied by dependent yearlings (keeping females) and the following year, when they have separated from their 2-year-old cubs in south-central Sweden, 2004-2016.**

		95% CI	
Model term	**β**	**Lower**	**Upper**
Intercept	-0.18	-0.40	0.05
Keeping female	0.13	-0.15	0.42
Distance to the nearest road	0.26	0.17	0.36
Distance to the nearest habitation	-0.09	-0.20	0.01
Mid-aged forest (1 vs 0)	-0.40	-0.67	-0.14
Old forest (1 vs 0)	0.76	0.51	1.01
Bog (1 vs 0)	-0.38	-0.73	-0.03
Clearcut (1 vs 0)	0.66	0.21	1.11
Keeping female * Distance to the nearest road	0.20	0.07	0.32
Keeping female * Distance to the nearest habitation	0.27	0.14	0.40
Keeping female * Mid-aged forest (1 vs 0)	0.06	-0.27	0.39
Keeping female * Old forest (1 vs 0)	-0.28	-0.59	0.03
Keeping female * Bog (1 vs 0)	-0.14	-0.58	0.29
Keeping female * Clearcut (1 vs 0)	-0.61	-1.20	-0.03

Continuous variables were scaled. The signs of β coefficients for "distance to" variables were reversed for ease of interpretation. Positive coefficients ($\beta > 0$) indicate selection, negative coefficients ($\beta < 0$) indicate avoidance, and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to availability.

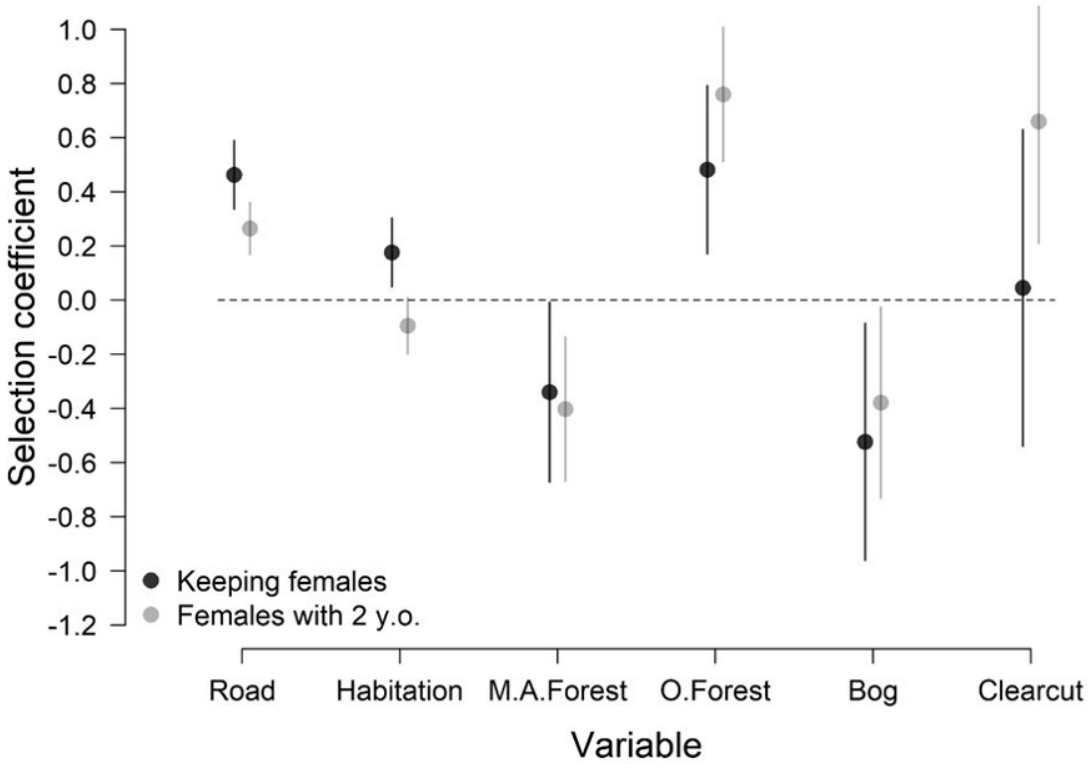

Figure A4.3 Changes in habitat selection coefficients (and 95% confidence intervals) of brown bear females (n=4) between the year they were accompanied by dependent yearlings (keeping females) and the following year, when they have separated from their 2-year-old cubs in south-central Sweden, 2004-2016.

Positive coefficients ($\beta > 0$) indicate selection, negative coefficients ($\beta < 0$) indicate avoidance, and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to what is available. Definitions: "Road" = distance to the nearest road, "Habitation" = distance to the nearest human habitation, "M.A.Forest" = mid-aged forest, "O.Forest" = old forest, "Bog" = bogs and tree-rich bogs, "Clearcut" = recently cut forest stand. The signs of "distance to" variables were reversed for ease of interpretation.

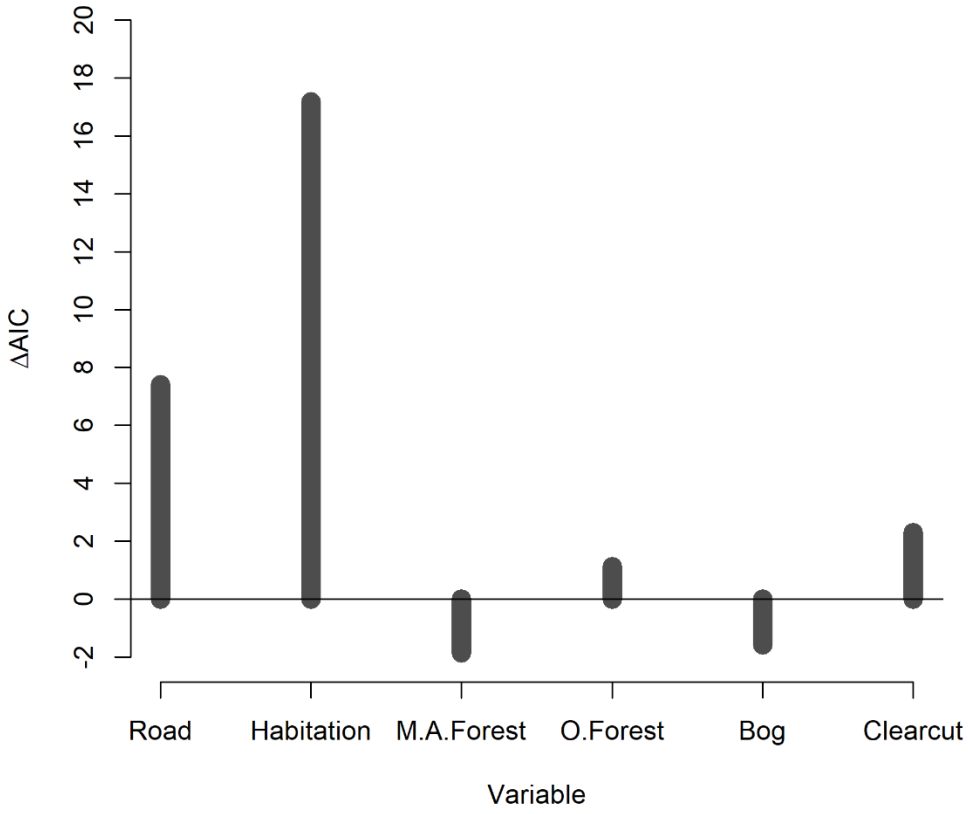

Figure A4.4 Change in AIC after the removal of an interaction term with "group" (2 levels factor: keeping females and females with 2-year-olds) for each variable in the global model explaining resource selection of female brown bears in south-central Sweden, 2004-2016.

Only females that were monitored both when accompanied by dependent yearlings and the following year, when they have separated from their 2-year-old cubs were included in the model (n=4 females, corresponding to 8 bear-years). Large and positive ΔAIC values suggest large between-group differences in resource selection for the variables tested, whereas negative values suggest poorer model fit. Definitions: "Road" = distance to the nearest road, "Habitation" = distance to the nearest human habitation, "M.A.Forest" = mid-aged forest, "O.Forest" = old forest, "Bog" = bogs and tree-rich bogs, "Clearcut" = recently cut forest stand.

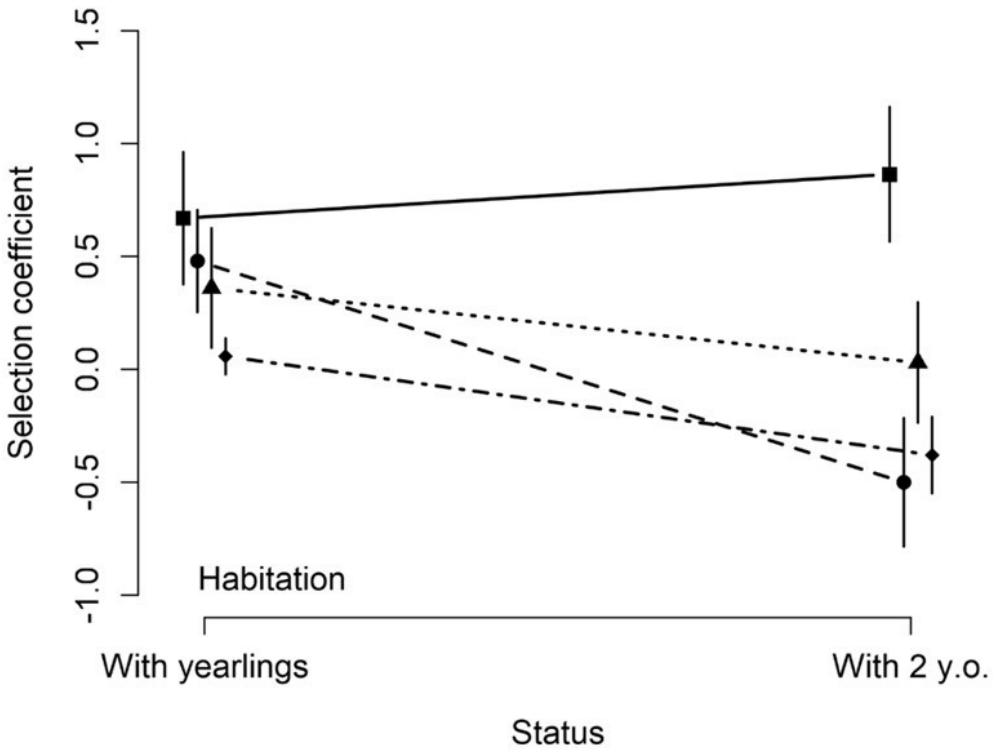

Figure A4.5 Change in selection (selection coefficient and 95% confidence intervals) for human habitation of brown bear females (n=4) between the year they were accompanied by dependent yearlings ("With yearlings") and the following year, when they have separated from their 2-year-olds ("With 2 y.o.") during the mating season in south-central Sweden, 2004-2016.

Each line represents a different individual female. Positive coefficients ($\beta > 0$) indicate selection, negative coefficients ($\beta < 0$) indicate avoidance, and null coefficients (95% confidence interval of β includes 0) mean that resources are used in proportion to what is available.

7.4 Annexe Chapitre 5

7.4.1 Appendix 5.1: Supplementary tables and figures

Table A5.1 Empirical demographic rates of brown bear females in south-central Sweden from 1993-2015

	1.5-year tactic			2.5-year tactic			All females*		
Demographic rate	Mean	SE	n	Mean	SE	N	Mean	SE	n
S_1	0.780	0.038	118	1.000	0.000	32	0.827	0.031	150
S_2	0.860	0.037	86	0.862	0.064	29	0.866	0.031	119
S_3	0.931	0.030	72	0.895	0.070	19	0.919	0.027	99
$S_{4\text{-}8}$	0.973	0.013	149	0.985	0.015	65	0.911	0.015	370
S_{9+}	0.841	0.027	182	0.916	0.027	107	0.831	0.020	355
$R_{5\text{-}9}$	0.327	0.051	147	0.297	0.091	64	0.241	0.035	278
R_{10+}	0.471	0.068	140	0.233	0.057	90	0.367	0.047	237
λ†	1.090 [1.052, 1.127]			1.101 [1.040, 1.165]			1.031 [1.000, 1.062]		

Observed mean, standard error (SE), and sample size (n) of age-specific survival probability (S) and recruitment rate (R = number of female yearlings produced per female per year) along with resulting asymptotic population growth rate (λ) for the two maternal care tactics. Definitions: S_1 = survival of yearlings, S_2 = survival of 2 year-olds (y.o.), S_3 = survival of 3 y.o., $S_{4\text{-}8}$ = survival of 4-8 y.o., S_{9+} = survival of 9 y.o. and older, $R_{5\text{-}9}$ = recruitment of 5-9 y.o. and R_{10+} = recruitment of 10 y.o. and older. * For comparison, information is also provided for the entire population when considering all females within the population. This includes females that were excluded from the tactic-based models because we were unable to classify them within one tactic or the other due to, for example, an impossibility to determine weaning time. † λ here was calculated using observed demographic rates.

Table A5.2 **Estimates (β and 95% CI) of the effect of hunting pressure on the survival of female brown bears using either the 1.5-year or the 2.5-year maternal care tactics in south-central Sweden, 1993-2015**

	1.5-year tactic			2.5-year tactic		
Age-class	Mean	Lower	Upper	Mean	Lower	Upper
Yearling	-0.362	-5.552	4.993	-	-	-
2 y.o.	-8.264	-18.736	-0.087	-10.311	-32.032	7.549
3 y.o.	-11.176	-28.692	2.450	-12.517	-47.580	13.195
4-8 y.o.	-17.104	-41.043	-0.761	3.187	-25.622	30.478
9+ y.o.	-6.312	-12.617	-0.625	-2.907	-15.266	6.860

Posterior means of estimated effect sizes (log-odds) are given along with their 95% highest posterior density intervals. These effect sizes were used to make model predictions for a range of hunting pressures observed in the population between 1993-2015. For each hunting pressure simulated, predictions of survival probabilities were then back-transformed on the original scale and incorporated into hunting pressure-specific Leslie projection matrix models for each tactic to extract the asymptotic population growth rate.

Table A5.3 **Estimates (β and 95% CI) of the effect of population density on the survival probability of female brown bears using either the 1.5-year or the 2.5-year maternal care tactics in south-central Sweden, 1998-2015**

	1.5-year tactic			2.5-year tactic		
Age-class	Mean	Lower	Upper	Mean	Lower	Upper
Yearling	1.618	-0.2944	3.450	-	-	-
2 y.o.	0.522	-2.373	3.577	-9.448	-23.923	2.595
3 y.o.	0.562	-3.869	4.369	-0.008	-5.330	4.809
4-8 y.o.	1.712	-2.115	5.170	4.536	-4.782	14.139
9+ y.o.	-1.726	-3.536	0.030	-1.758	-6.260	2.928

Posterior means of estimated effect sizes (log-odds) are given along with their 95% highest posterior density intervals. These effect sizes were used to make model predictions for a range of population densities observed in the population between 1998-2015. For each population density simulated, predictions of survival probabilities were then back-transformed on the original scale and incorporated into population density-specific Leslie projection matrix models for each tactic to extract the asymptotic population growth rate.

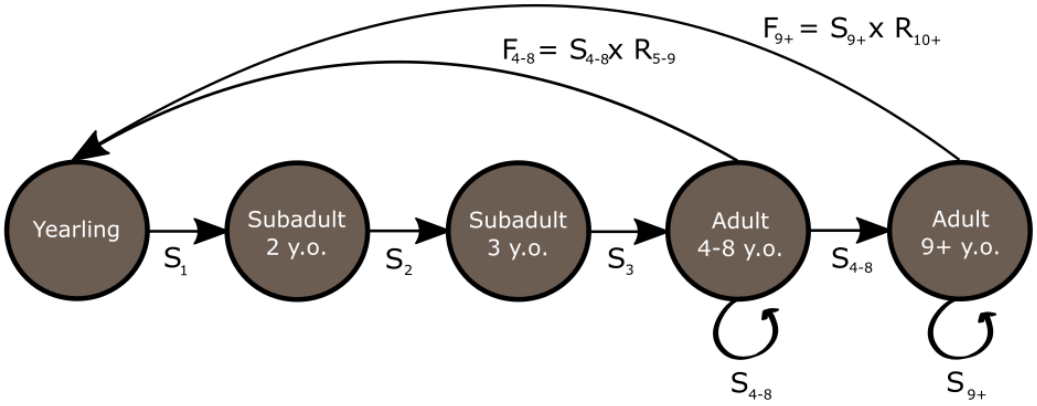

Figure A5.1 Life cycle graph of a female brown bear in Scandinavia.

The life cycle graph was used to construct age-structured population models. Definitions: S_1 = survival of yearlings, S_2 = survival of 2 y.o. (y.o. = years old), S_3 = survival of 3 y.o., S_{4-8} = survival of 4-8 y.o., S_{9+} = survival of 9 y.o. and older, S_{4-8} = fecundity of 4-8 y.o., F_{9+} = fecundity of 9 y.o. and older, R_{5-9} = recruitment of 5-9 y.o. and R_{10+} = recruitment of 10 y.o. and older.

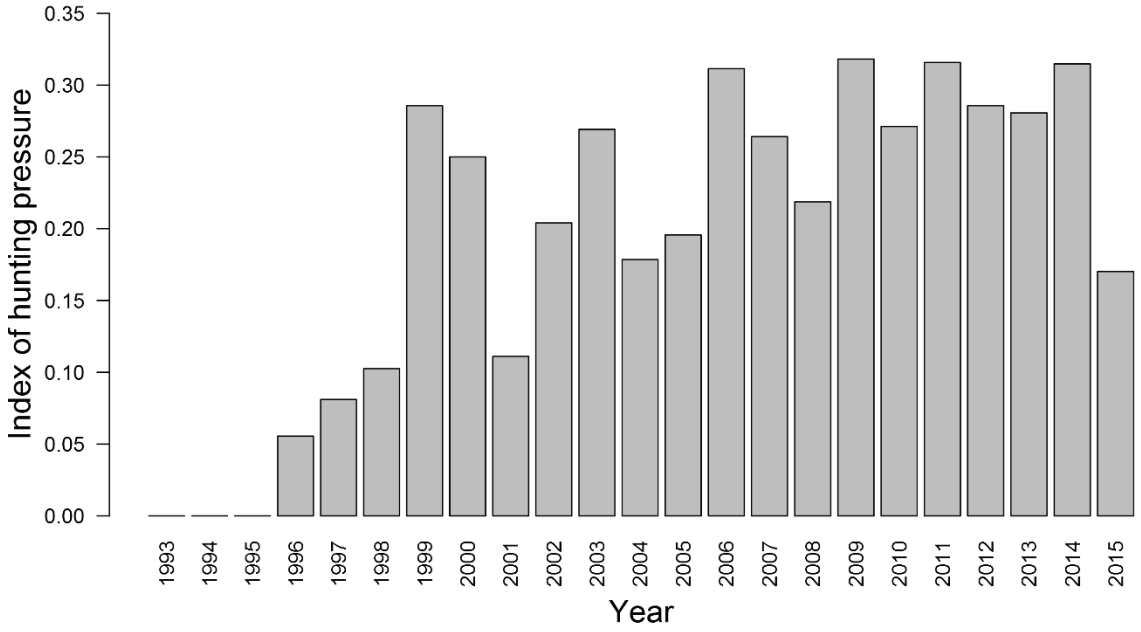

Figure A5.2 Annual index of bear hunting pressure in south-central Sweden from 1993-2015.

The index was estimated using all marked brown bears, i.e., by dividing the number of marked bears that were shot in a given year by the number of marked bears available for hunting that same year.

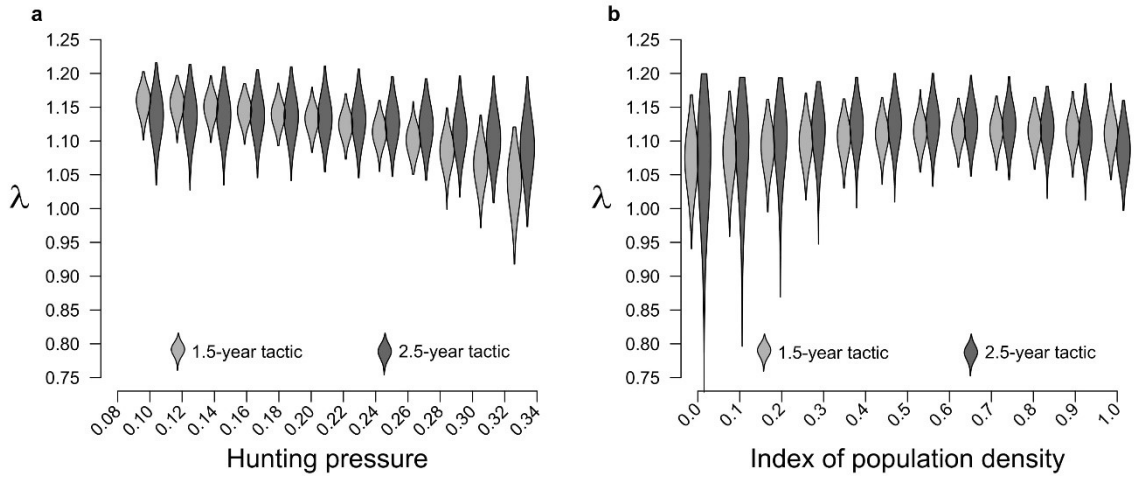

Figure A5.3 Effect of hunting pressure and population density on the fitness of female brown bears using either the 1.5-year or the 2.5-year maternal care tactic in south-central Sweden from 1998-2015.

Violin plots representing the predicted effects of **a** hunting pressure and **b** the index of population density on asymptotic population growth rate, λ, for each maternal care tactic. The violins represent the density plots of lambda (1,000 iterations) at each hunting pressure and population density index simulated. Because density could be estimated only for 1998-2015, the effect of hunting pressure over the same period is presented to provide adequate comparison. The effect of hunting pressure on tactic fitness considering the entire study period (1993-2015) is presented on Figure 5.1.

BIBLIOGRAPHIE

Agrell, J., Wolff, J.O., Ylönen, H. (1998). Counter-strategies to infanticide in mammals: costs and consequences. Oikos *83*, 507–517.

Allendorf, F.W., Hard, J.J. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. Proc. Natl. Acad. Sci. *106*, 9987–9994.

Andres, D., Clutton-Brock, T.H., Kruuk, L.E.B., Pemberton, J.M., Stopher, K.V., Ruckstuhl, K.E. (2013). Sex differences in the consequences of maternal loss in a long-lived mammal , the red deer (*Cervus elaphus*). Behav. Ecol. Sociobiol. *67*, 1249–1258.

Arnemo, J.M., Evans, A., Fahlman, Å. (2011). Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx (Evenstad, Norway: Hedmark University College).

Arnqvist, G., Rowe, L. (2005). Sexual conflict (Princeton, New Jersey: Princeton University Press).

Bădescu, I., Katzenberg, M.A., Watts, D.P., Sellen, D.W. (2017). A novel fecal stable isotope approach to determine the timing of age-related feeding transitions in wild infant chimpanzees. Am. J. Phys. Anthropol. *162*, 285–299.

Balme, G.A., Batchelor, A., De Woronin Britz, N., Seymour, G., Grover, M., Hes, L., MacDonald, D.W., Hunter, L.T.B. (2013). Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. Mamm. Rev. *43*, 221–237.

Balme, G.A., Robinson, H.S., Pitman, R.T., Hunter, L.T.B. (2017). Flexibility in the duration of parental care: female leopards prioritise cub survival over reproductive output. J. Anim. Ecol. *86*, 1224–1234.

Bateman, P.W., Fleming, P.A. (2012). Big city life: carnivores in urban environments. J. Zool. *287*, 1–23.

Bellemain, E., Swenson, J.E., Taberlet, P. (2006). Mating strategies in relation to sexually selected infanticide in a non-social carnivore: the brown bear. Ethology *112*, 238–246.

Bernardo, J. (1996). The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. Am. Zool. *36*, 216–236.

Bieber, C., Ruf, T. (2005). Population dynamics in wild boar Sus scrofa: ecology, elasticity of growth rate and implications. J. Appl. Ecol. *42*, 1203–1213.

Bischof, R., Bonenfant, C., Rivrud, I.M., Zedrosser, A., Friebe, A., Coulson, T., Mysterud, A., Swenson, J. E. (2018). Regulated hunting re-shapes the life history of brown bears. Nat. Ecol. Evol. *2*, 116–123.

Bischof, R., Fujita, R., Zedrosser, A., Söderberg, A., Swenson, J.E. (2008). Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. J. Wildl. Manage. *72*, 79–88.

Bischof, R., Swenson, J.E., Yoccoz, N.G., Mysterud, A., Gimenez, O. (2009). The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. J. Anim. Ecol. *78*, 656–665.

Bjärvall, A. (1990). The brown bear in Sweden. Aquilo Ser. Zool. *27*, 17–19.

Borries, C., Koenig, A., Winkler, P. (2001). Variation of life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). Behav. Ecol. Sociobiol. *50*, 391–402.

Borries, C., Lu, A., Ossi-Lupo, K., Larney, E., Koenig, A. (2014). The meaning of weaning in wild Phayre's leaf monkeys: last nipple contact, survival, and independence. Am. J. Phys. Anthropol. *154*, 291–301.

Bunnefeld, N., Baines, D., Newborn, D., Milner-Gulland, E.J. (2009). Factors affecting unintentional harvesting selectivity in a monomorphic species. J. Anim. Ecol. *78*, 485–492.

Cameron, E.Z. (1998). Is suckling behaviour a useful predictor of milk intake ? A review. Anim. Behav. *56*, 521–532.

Caswell, H. (2001). Matrix population models: construction, analysis, and interpretation (Sunderland, MA: Sinauer Associates).

Charnov, E.L., Ernest, S.K.M. (2006). The offspring-size/clutch-size trade-off in mammals. Am. Nat. *167*, 578–582.

Chiyo, P.I., Obanda, V., Korir, D.K. (2015). Illegal tusk harvest and the decline of tusk size in the African elephant. Ecol. Evol. *5*, 5216–5229.

Ciuti, S., Muhly, T.B., Paton, D.G., McDevitt, A.D., Musiani, M., Boyce, M.S. (2012). Human selection of elk behavioural traits in a landscape of fear. Proc. R. Soc. B. *279*, 4407–4416.

Clutton-Brock, T.H. (1991). The evolution of parental care (Princeton, New Jersey: Princeton University Press).

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C., Festa-Bianchet, M. (2003). Undesirable evolutionary consequences of trophy hunting. Nature *426*, 655–658.

Coulson, T., Godfray, H.C.J. (2007). Single-species dynamics. In Theoretical ecology, R. May, A. McLean, eds. (Oxford: Oxford University Press), pp. 17-34.

Craighead, J.J., Sumner, J.S., Mitchell, J.A. (1995). The grizzly bears of Yellowstone. Their ecology in the Yellowstone ecosystem (Washington DC, USA: Island Press).

Dahle, B., Swenson, J.E. (2003a). Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring. Behav. Ecol. Sociobiol. *54*, 352–358.

Dahle, B., Swenson, J.E. (2003b). Family break-up in brown bears: are young forced to leave? J. Mammal. *84*, 536–540.

Dahle, B., Swenson, J.E. (2003c). Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. J. Zool. *260*, 329–335.

Dahle, B., Zedrosser, A., Swenson, J.E. (2006). Correlates with body size and mass in yearling brown bears (*Ursus arctos*). J. Zool. *269*, 273–283.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E., Wilmers, C.C. (2009). Human predators outpace other agents of trait change in the wild. Proc. Natl. Acad. Sci. *106*, 952–954.

Darwin, C. (1859). On the origin of species (London: John Murray).

Davies, N.B., Krebs, J.R., West, S.A. (2012). An introduction to behavioural ecology (Oxford: Wiley-Blackwell).

Dawkins, R., Carlisle, T.R. (1976). Parental investment, mate desertion and a fallacy. Nature *262*, 131–133.

Derocher, A.E., Andriashek, D., Arnould, J.P.Y. (1993). Aspects of milk composition and lactation in polar bears. Can. J. Zool. *71*, 561–567.

DeWitt, T.J., Schneider, S.M. (2004). Phenotypic plasticity: functional and conceptual approached (New-York, NY: Oxford University Press).

Eberhardt, L.L. (2002). A paradigm for population analysis of long-lived vertebrates. Ecology *83*, 2841–2854.

Ericsson, G. (2001). Reduced cost of reproduction in moose *Alces alces* through human harvest. Alces *37*, 61–69.

Esteruelas, N.F. 2017. Short and long-term physiological effects of capture and handling on free-ranging brown bears (*Ursus arctos*). Thèse de doctorat. Inland Norway University of Applied Sciences, Evenstad.

Fairbanks, L.A., McGuire, M.T. (1995). Maternal condition and the quality of maternal care in vervet monkeys. Behaviour *132*, 733–754.

Falconer, D.S., Mackay, T.F. C. (1996). Introduction to quantitative genetics (Essex, U.K.: Longman).

Farley, S.D., Robbins, C.T. (1995). Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can. J. Zool. *73*, 2216–2222.

Fenberg, P.B., Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Mol. Ecol. *17*, 209–220.

Festa-Bianchet, M. (2003). Exploitative wildlife management as a selective pressure for the life-history evolution of large mammals. In Animal behavior and wildlife conservation, M. Festa-Bianchet, M. Apollonio, eds. (Washington DC, USA: Island Press).

Festa-Bianchet, M., Côté, S.D., Hamel, S., Pelletier, F. (2019). Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction. J. Anim. Ecol. *88*, 118–1133.

Festa-Bianchet, M., Jorgenson, J.T. (1998). Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behav. Ecol. *9*, 144–150.

Festa-Bianchet, M., Jorgenson, J.T., Wishart, W.D. (1994). Early weaning in bighorn sheep, Ovis canadensis, affects growth of males but not of females. Behav. Ecol. *5*, 21–27.

Fox, C.W., Westneat, D.F. (2010). Adaptation. In Evolutionary behavioral ecology, D. Westneat, C.W. Fox, eds. (New-York, NY: Oxford University Press), pp. 16-31.

Frank, S.C., Leclerc, M., Pelletier, F., Rosell, F., Swenson, J.E., Bischof, R., Kindberg, J., Eiken, H.G., Hagen, S.B., Zedrosser, A. (2018). Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. J. Anim. Ecol. *87*, 247–258.

Frank, S.C., Ordiz, A., Gosselin, J., Hertel, A., Kindberg, J., Leclerc, M., Pelletier, F., Steyaert, S.M.J.G., Støen, O.-G., Van de Walle, J. (2017). Indirect effects of bear hunting: a review from Scandinavia. Ursus *28*, 150–164.

Freeman, S., Herron, J.C. (2007). Evolutionary analysis (New Jersey, NJ: Pearson Prentice Hall).

Friebe, A., Evans, A.L., Arnemo, J.M., Blanc, S., Brunberg, S., Fleissner, G., Swenson, J.E., Zedrosser, A. (2014). Factors affecting date of implantation, parturition, and den entry estimated from activity and body temperature in free-ranging brown bears. PLoS ONE, *9*, e101410.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecol. Evol. *13*, 58–63.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. Annu. Rev. Ecol. Syst. *31*, 367–393.

Gélin, U., Wilson, M.E., Coulson, G., Festa-Bianchet, M. (2015). Experimental manipulation of female reproduction demonstrates its fitness costs in kangaroos. J. Anim. Ecol. *84*, 239–248.

Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A., Merilä, J. (2008). Climate change and evolution: disentangling environmental and genetic responses. Mol. Ecol. *17*, 167–178.

Gittleman, J.L., Thompson, S.D. (1988). Energy allocation in mammalian reproduction. Am. Zool. *28*, 863–875.

Gonzalez, O., Zedrosser, A., Pelletier, F., Swenson, J.E., Festa-Bianchet, M. (2012). Litter reductions reveal a trade-off between offspring size and number in brown bears. Behav. Ecol. Sociobiol. *66*, 1025–1032.

Gosselin, J., Leclerc, M., Zedrosser, A., Steyaert, S.M.J.G., Swenson, J.E., Pelletier, F. (2017). Hunting promotes sexual conflict in brown bears. J. Anim. Ecol. *86*, 35–42.

Gosselin, J., Zedrosser, A., Swenson, J.E., Pelletier, F. (2015). The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. Proc. R. Soc. B. *282*, 20141840.

Gross, M.R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol. Evol. *11*, 92–98.

Grüebler, M.U., Naef-Daenzer, B. (2008). Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. Ecology *89*, 2736–2745.

Grüebler, M.U., Naef-Daenzer, B. (2008). Postfledging parental effort in barn swallows: evidence for a trade-off in the allocation of time between broods. Anim. Behav. *75*, 1877–1884.

Hamel, S., Gaillard, J.-M., Festa-Bianchet, M., Côté, S.D. (2009). Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology *90*, 1981–1995.

Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Loison, A., Bonenfant, C., Descamps, S. (2010). Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecol. Lett. *13*, 915–935.

Hamilton, W.D. (1964). The genetical evolution of social behavior II. J. Theor. Biol. *7*, 17–52.

Harris, R.B., Wall, W.A., Allendorf, F.W. (2002). Genetic consequences of hunting: what do we know and what should we do? Wildl. Soc. Bull. *30*, 634–643.

Hebblewhite, M., Haydon, D.T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philos. Trans. R. Soc. B. Biol. Sci. *365*, 2303–2312.

Heino, M., Pauli, B.D., Dieckmann, U. (2015). Fisheries-induced evolution. Annu. Rev. Ecol. Evol. Syst. *46*, 461–480.

Hendry, A.P., Kinnison, M.T. (1999). The pace of modern life measuring rates of contemporary microevolution. Evolution *53*, 1637–1653.

Hertel, A.G., Zedrosser, A., Mysterud, A., Støen, O.-G., Steyaert, S.M.J.G., Swenson, J.E. (2016). Temporal effects of hunting on foraging behavior of an apex predator: do bears forego foraging when risk is high? Oecologia *182*, 1019–1029.

Hilderbrand, G.V., Schwartz, C.C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S.M., Servheen, C. (1999). The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can. J. Zool. *77*, 132–138.

Hofer, H., East, M.L. (2003). Behavioral processes and cost of co-existence in female spotteds hyenas: a life history perspective. Evol. Ecol. *17*, 315–331.

Hrdy, S.B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol. Sociobiol. *1*, 13–40.

Hunter, C.M., Caswell, H., Runge, M.C., Regehr, E.V., Amstrup, S.C., Stirling, I. (2010). Climate change threatens polar bear populations: a stochastic demographic analysis. Ecology *91*, 2883–2897.

Jennions, M.D., Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. Biol. Rev. *75*, 21–64.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S. *et al.* (2007). Managing evolving fish stocks. Science *318*, 1247–1248.

Kamel, S.J., Williams, P.D. (2017). Resource exploitation and relatedness: implications for offspring size variation within broods. Oikos *126*, 1219–1226.

Kindberg, J., Swenson, J.E. (2006). Results from the genetic analyses performed on feces samples from bears in Västerbotten County, Sweden. Part II Population estimate. Report No. 2006-3 from the Scandinavian Brown Bear Research Project.

Kohlmann, S.G., Green, R.L., Trainer, C.E. (1999). Effects of collection method on sex and age composition of black bear (*Ursus americanus*) harvest in Oregon. Northwest Sci. *73*, 34–38.

Kokko, H., Jennions, M.D. (2008). Parental investment, sexual selection and sex ratios. J. Evol. Biol. *21*, 919–948.

Krofel, M., Jonozovič, M., Jerina, K. (2012). Demography and mortality patterns of removed brown bears in a heavily exploited population. Ursus *23*, 91–103.

Kruuk, L.E.B., Clutton-Brock, T.H., Slate, J., Pemberton, J.M., Brotherstone, S., Guinness, F.E. (2000). Heritability of fitness in a wild mammal population. Proc. Natl. Acad. Sci. *97*, 698–703.

Kvarnemo, C. (2010). Parental care. In Evolutionary behavioral ecology, D. Westneat, C. W. Fox, eds. (New York, NY: Oxford University Press), pp. 451-470.

Lambert, Y. (2013). Long-term changes in life history characteristics and reproductive potential of northern Gulf of St. Lawrence cod (*Gadus morhua*) and consequences for the stock productivity. Fish. Res. *138*, 5–13.

Langer, P. (2003). Lactation, weaning period, food quality, and digestive tract differentiations in eutheria. Evolution *57*, 1196–1215.

Lavigne, L., Barrette, C. (1992). Suckling, weaning, and growth in captive woodland caribou. Can. J. Zool. *70*, 1753–1766.

Law, R. (2000). Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science *57*, 659–668.

Leclerc, M., Frank, S.C., Zedrosser, A., Swenson, J.E., Pelletier, F. (2017). Hunting promotes spatial reorganization and sexually selected infanticide. Sci. Rep. *7*, 45222.

Leclerc, M., Van de Walle, J., Zedrosser, A., Swenson, J.E., Pelletier, F. (2016). Can hunting data be used to estimate unbiased population parameters? A case study on brown bears. Bio. Lett. *12*, 20160197.

Leclerc, M., Zedrosser, A., Pelletier, F. (2017). Harvesting as a potential selective pressure on behavioural traits. J. Appl. Ecol. *54*, 1941–1945.

Leclerc, M., Zedrosser, A., Swenson, J.E., Pelletier, F. (2019). Hunters select for behavioral traits in a large carnivore. Sci. Rep. *9*, 12371.

Lee, P.C. (1996). The meanings of weaning: growth, lactation, and life history. Evol. Anthropol. *5*, 87–98.

Lee, P.C., Majluf, P., Gordon, I.J. (1991). Growth, weaning and maternal investment from a comparative perspective. J. Zool. London *225*, 99–114.

Lee, P.C., Moss, C.J. (1986). Early maternal investment in male and female African elephant calves. Behav. Ecol. Sociobiol. *18*, 353–361.

Lessels, C.M. (1999). Sexual conflict in animals. In Levels of selection in evolution, L. Keller, ed. (Princeton, New Jersey, NY: Princeton University Press), pp. 75-99.

Lindström, J. (1999). Early development and fitness in birds and mammals. Trends Ecol. Evol. *14*, 343–348.

Lonsdorf, E.V., Stanton, M.A., Pusey, A.E., Murray, C.M. (2019). Sources of variation in weaned age among wild chimpanzees in Gombe National Park, Tanzania. Am. J. Phys. Anthropol. *171*, 419–429.

Majerus, M.E.N. (2009). Industrial melanism in the peppered moth, *Biston betularia*: an excellent teaching example of Darwinian evolution in action. Evol. Educ. Outreach *2*, 63–74.

Manchi, S., Swenson, J.E. (2005). Denning behaviour of Scandinavian brown bears Ursus arctos. Wildl. Biol. *11*, 123–132.

Mclellan, B.N., Hovey, F.W., Mace, R.D., Woods, J.G., Carney, D.W., Gibeau, M.L., Wakkinen, W.L., Kasworm, W.F. (1999). Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. J. Wildl. Manage. *63*, 911–920.

McLellan, B.N., Shackleton, D.M. (1988). A comparison of grizzly bear harvest data from Montana and southeastern British Columbia. Wildl. Soc. Bull. *16*, 371–375.

Merilä, J., Hendry, A.P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evol. Appl. *7*, 1–14.

Merilä, J., Sheldon, B.C., Kruuk, L.E.B. (2001). Explaining stasis: microevolutionary studies in natural populations. Genetica (112–113), 199–222.

Miller, S.D. (1990). Population management of bears in North America. Int. Conf. Bear Res. Manag. *8*, 357–373.

Milner, J.M., Nilsen, E.B., Andreassen, H.P. (2007). Demographic side effects of selective hunting in ungulates and carnivores. Conserv. Biol. *21*, 36–47.

Morino, L., Borries, C. (2017). Offspring loss after male change in wild siamangs: the importance of abrupt weaning and male care. Am. J. Phys. Anthropol. *162*, 180–185.

Muelbert, M.M.C., Bowen, W.D. (1993). Duration of lactation and postweaning changes in mass and body composition of harbour seal, *Phoca vitulina*, pups. Can. J. Zool. *71*, 1405–1414.

Mysterud, A. (2011). Selective harvesting of large mammals: how often does it result in directional selection? J. Appl. Ecol. *48*, 827–834.

Nawaz, M.A., Swenson, J.E., Zakaria, V. (2008). Pragmatic management increases a flagship species, the Himalayan brown bears, in Pakistan's Deosai National Park. Biol. Conserv. *141*, 2230–2241.

Ordiz, A., Støen, O.-G., Sæbø, S., Kindberg, J., Delibes, M., Swenson, J.E. (2012). Do bears know they are being hunted? Biol. Conserv. *152*, 21–28.

Otto, S., Day, T. (2007). A biologist's guide to mathematical modeling in ecology and evolution (New Jersey: Princeton University Press).

Palombit, R.A. (2015). Infanticide as sexual conflict: coevolution of male strategies and female counterstrategies. Cold Spring Harb. Perspect. Biol. *7*, a017640.

Palumbi, S.R. (2001). Humans as the world's greatest evolutionary force. Science *293*, 1786–1790.

Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T., Ozgul, A. (2019). Life history responses of meerkats to seasonal changes in extreme environments. Science *363*, 631–635.

Paniw, M., Ozgul, A., Salguero-Gómez, R. (2018). Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. Ecol. Lett. *21*, 275–286.

Parker, G. (1979). Sexual selection and sexual conflict. In Sexual selection and reproductive competition in insects, M.S., Blum, N.A. Blum, eds. (London, UK: Academic Press), pp. 123-166.

Pasitschniak-Arts, M. (1993). Mammalian species: *Ursus arctos*. Ame. Soc. Mammal. *439*, 1–10.

Pelletier, F., Coltman, D.W. (2018). Will human influences on evolutionary dynamics in the wild pervade the Anthropocene? BMC Biol. *16*, 7.

Pelletier, F., Moyes, K., Clutton-brock, T.H., Coulson, T. (2011). Decomposing variation in population growth into contributions from environment and phenotypes in an age-structured population. Proc. R. Soc. B. *279*, 394–401.

Pianka, E.R. (1970). On r- and K-selection. Am. Nat. *104*, 592–597.

Pianka, E.R. (1976). Natural selection of optimal reproductive tactics. Am. Zool. *16*, 775–784.

Pigeon, G., Festa-Bianchet, M., Coltman, D.W., Pelletier, F. (2016). Intense selective hunting leads to artificial evolution in horn size. Evol. Appl. *9*, 521–530.

Postma, E. (2014). Four decades of estimating heritabilities in wild vertebrate populations: improved methods, more data, better estimates? In Quantitative genetics in the wild, A. Charmantier, D. Garant, L.E.B Kruuk, eds. (New-York, NY: Oxford University Press), pp. 16-33.

Quesnel, H., Prunier, A. (1995). Endocrine bases of lactational anoestrus in the sow. Reprod. Nutr. Dev. *35*, 395–414.

Réale, D., Festa-Bianchet, M. (2000). Mass-dependent reproductive strategies in wild bighorn ewes: a quantitative genetic approach. J. Evol. Biol. *13*, 679–688.

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V., Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. Phil. Trans. R. So. London. Ser. B. *365*, 4051–4063.

Rivrud, I.M., Frank, S.C., Bischof, R., Mysterud, A., Steyaert, S.M.J.G., Hertel, A.G., Hagen, S.B., Eiken, H.G., Swenson, J.E., Zedrosser, A. (2019). Heritability of head size in a hunted large carnivore, the brown bear (*Ursus arctos*). Evol. Appl. *12*, 1124–1135.

Rughetti, M., Festa-Bianchet, M. (2011). Effects of early horn growth on reproduction and hunting mortality in female chamois. J. Anim. Ecol. *80*, 438–447.

Rughetti, M., Festa-Bianchet, M. (2014). Effects of selective harvest of non-lactating females on chamois population dynamics. J. Appl. Ecol. *51*, 1075–1084.

Sadleir, R.M.F.S. (1980). Energy and protein intake in relation to growth of suckling black-tailed deer fawns. Can. J. Zool. *58*, 1347–1354.

Saether, B.-E. (1997). Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends Ecol. Evol. *12*, 143–149.

Sæther, B.-E., Coulson, T., Grøtan, V., Engen, S., Altwegg, R., Armitage, K.B., Barbraud, C., Becker, P.H., Blumstein, D.T., Dobson, F.S., *et al.* (2013). How life history influences population dynamics in fluctuating environments. Am. Nat. *182*, 743–759.

Saether, B.-E., Engen, S., Swenson, J.E., Bakke, O., Sandegren, F. (1998). Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations the effects of uncertain parameter estimates. Oikos *83*, 403–416.

Schwartz, C.C., Miller, S.D., Haroldson, M.A. (2003). Grizzly bear. In Wild mammals of North America: biology, management and conservation, G.A. Feldhammer, B.C. Thompson, J.A. Chapman, eds. (Baltimore, MD, USA: The John Hopkins University Press).

Seamans, M.E., Gutiérrez, R.J., May, C.A., Peery, M.Z. (1999). Demography of two Mexican spotted owl populations. Conserv. Biol. *13*, 744–754.

Servanty, S., Gaillard, J.-M., Ronchi, F., Focardi, S., Baudet, É., Gimenez, O. (2011). Influence of harvesting pressure on demographic tactics: implications for wildlife management. J. Appl. Ecol. *48*, 835–843.

Sibly, R.M., Hone, J. (2002). Population growth rate and its determinants: an overview. Philos. Trans. R. Soc. London B. *357*, 1153–1170.

Sikes, R.S. (1998). Tradeoffs between quality of offspring and litter size: differences do not persist into adulthood. J. Mammal. *79*, 1143–1151.

Sinclair, A.R E., Pech, R.P. (1996). Density dependence, stochasticity, compensation and predator regulation. Oikos *75*, 164–173.

Sinervo, B., Svensson, E., Comendant, T. (2000). Density cycles and an offspring quantity and quality game driven by natural selection. Nature *406*, 985–988.

Smiseth, P.T., Kölliker, M., Royle, N.J. (2012). What is parental care? In The evolution of parental care, N.J. Royle, P.T. Smiseth, M. Kölliker, eds. (Oxford, UK: Oxford University Press), pp. 1-20.

Smith, T.M., Austin, C., Hinde, K., Vogel, E. R., Arora, M. (2017). Cyclical nursing patterns in wild orangutans. Sci. Adv. *3*, e1601517.

Solberg, E.J., Loison, A., Saether, B.-E., Strand, O. (2000). Age-specific harvest mortality in a Norwegian moose Alces alces population. Wildl. Biol. *6*, 41–52.

Spady, T.J., Lindburg, D.G., Durrant, B.S. (2007). Evolution of reproductive seasonality in bears. Mamm. Rev. *37*, 21–53.

Stearns, S.C. (1989). Trade-offs in life-history evolution. Funct. Ecol. *3*, 259–268.

Stearns, S.C. (1992). The evolution of life histories (Oxford, UK: Oxford University Press).

Steyaert, S.M.J.G., Kindberg, J., Swenson, J.E., Zedrosser, A. (2013). Male reproductive strategy explains spatiotemporal segregation in brown bears. J. Anim. Ecol. *82*, 836–845.

Steyaert, S.M.J.G., Endrestøl, A., Hackländer, K., Swenson, J.E., Zedrosser, A. (2012). The mating system of the brown bear *Ursus arctos*. Mamm. Rev. *42*, 12–34.

Steyaert, S.M.J.G., Leclerc, M., Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J.E., Zedrosser, A. (2016). Human shields mediate sexual conflict in a top predator. Proc. R. Soc. B. *283*, 20160906.

Steyaert, S.M.J.G., Swenson, J.E., Zedrosser, A. (2014). Litter loss triggers estrus in a nonsocial seasonal breeder. Ecol. Evol. *4*, 300–310.

Støen, O.-G., Ordiz, A., Evans, A.L., Laske, T.G., Kindberg, J., Fröbert, O., Swenson, J.E., Arnemo, J. M. (2015). Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). Physiol. Behav. *152*, 244–248.

Swenson, J.E., Adamič, M., Huber, D., Stokke, S. (2007). Brown bear body mass and growth in northern and southern Europe. Oecologia *153*, 37–47.

Swenson, J.E., Sandegren, F. (1999). Conservation of European brown bear populations: experciences from Scandinavia. In La conservación del oso pardo en Europa: un reto de cara al siglo, J.F. Layna, B. Heredia, G.G. Palomero, eds. (Madrid, Spain), pp. 1-3.

Swenson, J.E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P., Franzén, R. (1994). Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. Biol. Conserv. *70*, 9–17.

Swenson, J.E., Sandegren, F., Bjärvall, A., Wabakken, P. (1998). Living with success: research needs for an expanding brown bear population. Ursus *10*, 17–23.

Swenson, J.E., Sandegren, F., Brunberg, S., Segerström, P. (2001). Factors associated with loss of brown bear cubs in Sweden. Ursus *12*, 69–80.

Swenson, J.E., Schneider, M., Zedrosser, A., Söderberg, A., Franzén, R., Kindberg, J. (2017). Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. Wildl. Biol. *2017*, wlb.00251.

Swenson, J.E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R., Söderberg, A. (1995). The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. Wildl. Biol. *1*, 11–25.

Tait, D.E.N. (1980). Abandonment as a reproductive tactic - The example of grizzly bears. Am. Nat. *115*, 800–808.

Tarwater, C.E., Brawn, J.D. (2010). The post-fledging period in a tropical bird: patterns of parental care and survival. J. Avian Biol. *41*, 479–487.

Trillmich, F. (1986). Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. Behav. Ecol. Sociobiol. *19*, 157–164.

Trillmich, F. (1990). The behavioral ecology of maternal effort in fur seals and sea lions. Behaviour *114*, 1–4.

Trillmich, F., Limberger, D. (1985). Drastic effects of El Niño on Galapagos pinnipeds. Oecologia *67*, 19–22.

Trivers, R.L. (1972). Parental investment and sexual selection. In Sexual selection and the descent of man, B. Campbell, ed. (Chicago, IL: Aldine Publishing Company), pp. 136-179.

Trivers, R.L. (1974). Parent-offspring conflict. Am. Zool. *14*, 249–264.

Turchin, P. (1999). Population regulation: a synthetic view. Oikos *84*, 153–159.

Van de Walle, J., Pigeon, G., Zedrosser, A., Swenson, J.E., Pelletier, F. (2018). Hunting regulation favors slow life histories in a large carnivore. Nat. Comm. *9*, 1100.

van Noordwijk, A.J., de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. *128*, 137–142.

van Wijk, S.J., Taylor, M.I., Creer, S., Dreyer, C., Rodrigues, F.M., Ramnarine, I.W., van Oosterhout, C., Carvalho, G. R. (2013). Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. Front. Ecol. Environ. *11*, 181–187.

Westneat, D., Fox, C.W. (2010). Evolutionary behavioral ecology (Oxford, NY: Oxford University Press)

Williams, G.C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. *100*, 687–690.

Wilson, A.J., Réale, D., Clements, M.N., Morrissey, M.M., Postma, E., Walling, C.A., Kruuk, L.E.B., Nussey, D.H. (2010). An ecologist' s guide to the animal model. J. Anim. Ecol. *79*, 13–26.

Zedrosser, A., Dahle, B., Støen, O.-G., Swenson, J.E. (2009). The effects of primiparity on reproductive performance in the brown bear. Oecologia *160*, 847–854.

Zedrosser, A., Dahle, B., Swenson, J.E. (2006). Population density and food conditions determine adult female body size in brown bears. J. Mammal. *87*, 510–518.

Zedrosser, A., Pelletier, F., Bischof, R., Festa-Bianchet, M., Swenson, J.E. (2013). Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations. Ecology *94*, 231–240.

Zedrosser, A., Steyaert, S.M.J.G., Gossow, H., Swenson, J.E. (2011). Brown bear conservation and the ghost of persecution past. Biol. Conserv. *144*, 2163–2170.

Zhao, Q., Borries, C., Pan, W. (2011). Male takeover, infanticide, and female countertactics in white-headed leaf monkeys (*Trachypithecus leucocephalus*). Behav. Ecol. Sociobiol. *65*, 1535–1547.

Zhao, Q., Tan, C.L., Pan, W. (2008). Weaning age, infant care, and behavioral development in *Trachypithecus leucocephalus*. Int. J. Primatol. *29*, 583–591.